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THE ARTERIES AND VEINS OF THE LUNGS

I. RIGHT UPPER LOBE

By A. B. APPLETON, *Department of Anatomy, St Thomas's Hospital Medical School*

The arrangement of the larger vessels within the lungs was described by Ewart (1888) and subsequently, without knowledge of his work, by Melnikoff (1924). Herrnheiser & Kubat (1936) later gave a description which took into account the work of Ewart and Melnikoff and in addition that of Backmann (1924). The veins were described by Adachi (1933) for Japanese subjects. These accounts, though detailed, lack precision as to the relations of vessels to those large subdivisions of the lung now known as bronchopulmonary segments to which Kramer & Glass (1932) first directed attention. Lucien & Weber (1936) have recognized similar subdivisions which they have grouped as 'territories of ventilation'.

The pattern of the bronchopulmonary segments depends on the mode of branching of the bronchial tree. Each segment is ventilated by a single bronchus which ventilates no other segment. The term bronchopulmonary segment has been restricted arbitrarily to those relatively large portions of lung which are ventilated by bronchi that have orifices into one of the lobar bronchi. These segments can be isolated from their neighbours by dissection with varying degrees of ease, since there are intervening planes of connective tissue, which will be here distinguished as the 'intersegmental planes'. Tributaries of the pulmonary veins lie in these planes and receive veins from the contiguous segments (Appleton, 1944). Each segment may be further divided into zones which are ventilated by the branches of the segmental bronchus (Foster Carter, 1942; Appleton, 1944). These will be termed 'subsegments'. The subsegments like the segments are separated by connective tissue planes, the subsegmental planes.

It is generally accepted that supernumerary fissures, clefts or notches tend to develop on the site of any of the intersegmental planes (Testut, 1930); they are also found sometimes on the sites of subsegmental planes (Appleton, 1944). The right and left lungs exhibit similar patterns of bronchopulmonary segments; the fissural pattern and the division into lobes is a superficial feature which is subject to individual variation without essential difference in the segmental pattern (Appleton, 1944). There is, however, individual variation in the relative size of a given segment (Brock, 1942).

The pattern of the bronchopulmonary segments described by Kramer & Glass, and by Glass (1934), has been accepted with modifications by subsequent British and American authors. The pattern described by Lucien & Weber has a different appearance, but its relation to that of Glass has been elucidated by Appleton (1944).

The observations of Ewart showed that the vascular pattern within the lung is closely related to that of the bronchi; this conclusion implies a relationship to the bronchopulmonary segments. Ewart found that the branches of the pulmonary artery follow the bronchi while the veins are by contrast spaced out between them. According to Miller, 1937, again, the collecting veins from the pulmonary unit or 'lobule' (ventilated by a terminal bronchiole) are situated peripherally to the lobule while branches of the pulmonary artery follow respiratory bronchioles to their final distribution. The consequence of this vascular pattern would be that the artery to a bronchopulmonary segment would be distributed within the segment along with the branches of the ventilating bronchus, while the veins would lie in the intervals between segments. Appleton (1944) has indeed observed that the main veins run on the periphery of segments, either between adjoining ones or on the pleural surfaces of the lungs.

The relation of vessels to segments is not, however, so clearly defined as these accounts suggest. Hovelacque, Monod & Evrard (1937) and Appleton (1944) have pointed out that although arteries in general accompany the bronchi very closely yet in the region of the hilum the arrangement of the arteries does not entirely reproduce the pattern of the bronchial tree. Narath (1901) showed that the same artery sometimes provides branches which are distributed with bronchi belonging to different parts of the bronchial tree, and both he and Melnikoff (1924) found that branches of the same bronchus are sometimes supplied by arteries with different origins from the pulmonary artery. The work of these authors thus showed some lack of correspondence between the arterial and the bronchial pattern.

Melnikoff (1924) recognized variability in the manner of origin of the larger vessels in the hilum, distinguishing 'magistral' and 'zertreut' types. Alternative names for these types have been offered by Herrnheiser & Kubat, who distinguish them as tree-like (dendroid) and bush-like (thamnoid) types. The accounts of these authors largely ignored the pattern of the bronchial tree. Melnikoff felt unable to adopt the well-known descriptions of the bronchial tree given by Aeby (1880) and Narath, who recognized a series of dorsal and ventral branches. He believed it would be more correct to describe the vessels,

especially the arteries, according to the lung regions they supply, in spite of differences of origin and calibre. Herrnheiser & Kubat have adopted a similar attitude (p. 601), inasmuch as various arteries supplying the posterior part of the upper lobe are identified by the same name 'A. axillaris' though their origins are widely different.

The account of the vascular arrangements of the segments in this paper will be given with reference to the descriptions of the segmental pattern given by Foster Carter (1942) and Appleton (1944). The arterial supply and venous drainage of the segments and subsegments are examined with special reference to recognition of the larger vessels with which they are connected in the hilum of the lung, as seen by approach to the lung root, anteriorly, posteriorly or through the interlobar fissures.

MATERIAL AND METHODS

The present description of the vascular pattern and its variations is based on a study of fifty adult right lungs. Of these, forty-five had been preserved *in situ* in cadavera prepared for the dissecting room. The remaining five were prepared from fresh post-mortem specimens.

They were examined by dissection from the mediastinal, costal and interlobar surfaces, supplemented in certain instances by horizontal slicing of the upper lobe. In twenty specimens injections of coloured gelatine were made into the arteries and veins; in the five fresh specimens these provided a complete injection of the vessels, in the remainder only a partial one of the larger vessels.

THE UPPER LOBE OF THE RIGHT LUNG

The pattern of the bronchi and bronchopulmonary segments of the upper lobe will be reviewed briefly, without attempt at a full account of the variations which have been summarized in a previous paper (Appleton, 1944). There has been much variation in the terminology employed by different authors as shown below.

Bronchi and bronchopulmonary segments. Names previously employed

Ewart	Pectoral	Apical		Axillary
Nelson	Pectoral	Apical		Axillary
Hasse	Anterior		Posterior	—
Kramer & Glass	Anterior	Apical	Posterior	Axillary
Lucien & Weber	Upper ventral	Apical	Upper dorsal	External Parabronchial
Neil, Gilmour & Gwynne	Anterior	Apical	Paravertebral	Axillary
Barrett	Pectoral	Apical	Posterior	Axillary
Peirce & Stocking	Ventral	Apical	Dorsal	—
Foster Carter	Anterolateral	Apical	Posterolateral	—
Brock	Pectoral	Apical	Subapical	—
Appleton	Pectoral	Apical	Posterior	—

The zone described as the axillary segment by earlier authors has been given a subsidiary status by later investigators, viz. that of subsegment or subsegments in one of the three larger zones (Appleton, 1944). Thus the posterior and anterior segments of Kramer & Glass are not entirely equivalent to the pectoral and subapical segments of Brock, but include portions only of these segments, the remaining portions being included under the heading 'axillary'.

The right upper lobe is divided, then, into three bronchopulmonary segments which will be termed pectoral, apical and posterior (cf. Fig. 13). These names have been selected from the various names that have been employed by different authors on the grounds of convenience, suitability and distinctive character (Appleton, 1944). They have proved adaptable to the naming of the arteries, veins, and intersegmental planes in such a way as to indicate the relations of the vessels to bronchopulmonary segments. The segments are ventilated by bronchi which arise from the upper lobe bronchus and bear the same names as the segments; they are separated by intersegmental planes which will be distinguished as the 'apicopectoral', 'apicoposterior' and 'pectoroposterior' planes. The term 'eparterial' in reference to the right upper lobe bronchus is rejected for reasons which have been stated by a succession of authors (Ewart, Narath, Brock).

Intersegmental planes (Figs. 1, 2, 6, 16 and 20)

The apicopectoral plane separates the apical and pectoral segments. It abuts on the mediastinal surface along a line that curves with an anterior convexity upwards from the root of the lung to reach the anterior margin, at or close to the subclavian groove. From this line the plane extends posterolaterally within the upper lobe, and the pectoral segment thus extends farther back on the costal than on the mediastinal surface.

The apicoposterior plane meets the mediastinal surface along an oblique line that passes upwards from the root of the lung to the margin just behind the apex. This plane is inclined posterolaterally towards the costal surface.

The pectoroposterior plane is orientated mediolaterally in the upper lobe, below the level of the

upper lobe bronchus. It meets the costal surface approximately opposite the junction of the oblique and horizontal fissures.

Bronchi (Figs. 6, 9, 16 and 17)

The pectoral, apical and posterior bronchi, which ventilate bronchopulmonary segments of the same names in the upper lobe, have their orifices at or

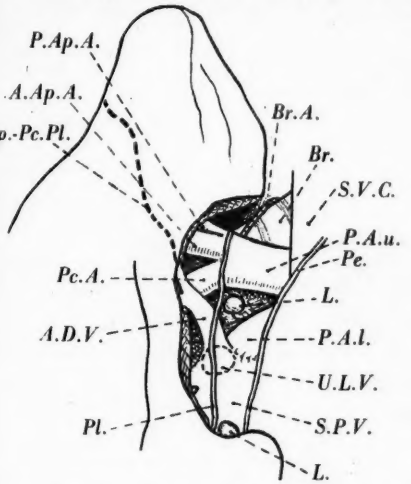


Fig. 1. Anterior exposure of the root of the right lung (upper part), to show courses of vessels after entering the upper lobe. *A.Ap.A.* anterior apical artery; *A.D.V.* anterior descending vein; *Ap.-Pc.Pl.* apicopectoral intersegmental plane; *Br.* right bronchus; *Br.A.* bronchial artery; *L.* lymph glands; *P.A.l.* right pulmonary artery, truncus inferior (connected by fascia to *S.P.V.*); *P.A.u.* pulmonary artery, truncus superior; *P.Ap.A.* posterior apical artery; *Pe.* pericardium (cut); *Pc.A.* pectoral artery; *Pl.* pleura (cut); *S.P.V.* superior pulmonary vein; *S.V.C.* superior vena cava; *U.L.V.* origin of great upper lobe vein.

close to the lateral end of the upper lobe bronchus. Variations in the arrangement of the orifices are common and have been described by Foster Carter (1942) and Appleton (1944).

The pectoral bronchus generally divides into 'pectoral axillary' and 'pectoral terminal'* bronchi (the 'anterolateral anterior' and 'anterolateral external' of Foster Carter), which respectively ventilate 'axillary' and 'terminal' subsegments. The pectoral terminal bronchus runs forwards close to the mediastinal surface towards the anterior margin of the lung and divides into superior and inferior branches. The pectoral axillary bronchus runs towards the costal surface and divides into superior (costal) and inferior (interlobar) bronchi of which the latter is close to the interlobar surface (Fig. 8). The pectoral axillary bronchus sometimes opens into the upper lobe bronchus directly (Foster Carter, Appleton), and the corresponding subsegment then attains the status of an independent axillary bronchopulmonary segment, an arrangement described as the usual one by Neil, Gilmour & Gwynne (1937).

The apical bronchus divides into 'anterior apical' and 'posterior apical' bronchi. Either the apical bronchus or one of its two branches gives off an 'apical axillary' bronchus directed posterolaterally to the costal surface.

The posterior bronchus divides into 'posterior axillary' and 'posterior terminal' bronchi. The latter is directed posterosuperiorly near the mediastinal surface and divides into superior and inferior terminal branches. The posterior axillary bronchus runs towards the costal surface, close at first to the interlobar surface, and divides into anterior and posterior branches; there is commonly an ascending 'costal' branch from the posterior branch.

Bronchopulmonary segments (Fig. 13)

The pectoral segment is the largest segment of the upper lobe, approximately forming that portion which is anterior to a plane through the subclavian groove and the junction of the horizontal and oblique fissures. Posteriorly it is bounded by the apicopectoral and pectoroposterior planes. It is wedge-shaped with an apex at the root of the lung, and it has interlobar, costal and mediastinal surfaces. It consists of 'terminal' and 'axillary' subsegments. The axillary subsegment forms a part of the interlobar surface above the posterior part of the horizontal fissure, and a part of the costal surface just above the same part of this fissure. The terminal subsegment forms the anterior part of the upper lobe including its anterior margin.

The apical segment is a wedge-shaped mass that includes the apex of the lung. It has an apex directed downwards towards the root of the lung. It consists of anterior, posterior and axillary subsegments. The two former adjoin along a plane passing downwards from the apex of the lung; together they constitute the mediastinal surface of the lung above its root. The anterior apical segment has an anterior extension on the mediastinal surface (Fig. 6). The apical axillary segment is exposed on the costal surface.

The posterior segment forms approximately that part of the upper lobe which is covered superficially

* The alternative names of 'costopectoral' and 'sternopectoral' respectively, employed by Herrnheiser & Kubat with reference to the accompanying arteries, might seem appropriate but are rejected on the following grounds: (1) the difficulty of finding a comparable terminology for the bronchi and arteries in the posterior segment, and (2) individual variation in which the origins of the axillary bronchi differ from the above account, more particularly on the left side (Appleton, 1944).

by the sacrospinalis muscle and scapula. It consists of 'terminal' and 'axillary' subsegments. The latter forms that part of the interlobar surface which is immediately behind the junction of horizontal and oblique fissures, and the adjacent costal surface. The terminal subsegment forms the region adjacent to the posterior pole of the upper lobe; it is exposed on the mediastinal surface behind the root of the lung and on the posterior parts of the interlobar and costal surfaces above the oblique fissure.

as the pectori-apical trunk, by Narath as the first branch of the pulmonary artery. Herrnheiser & Kubat described the right pulmonary artery as dividing into a 'truncus superior' and 'truncus intermedius', the continuation of the latter beyond the origin of the middle lobe arteries being distinguished as the 'truncus inferior'. The use of the term 'truncus intermedius' recalls Ewart's application of the term bronchus intermedius to the common stem which ventilates middle and lower lobes (and

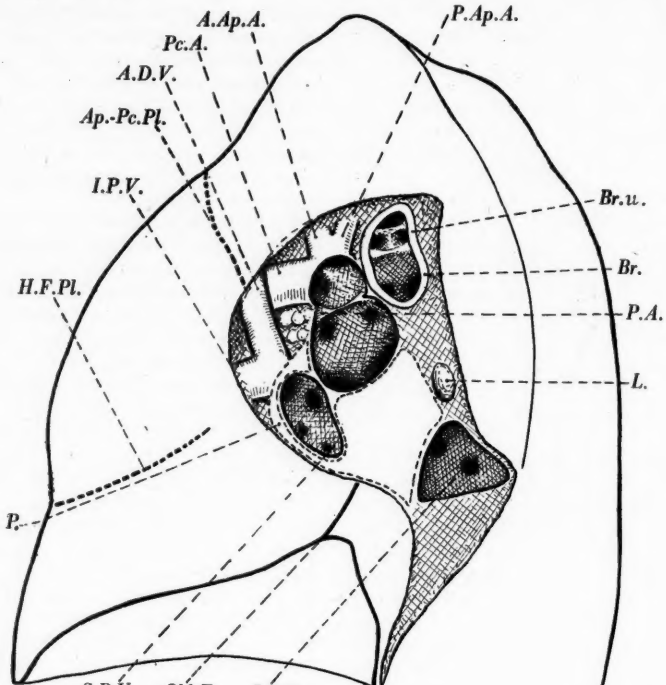


Fig. 2. Hilum of a right lung in which the lower part of the oblique fissure is the only fissure; medial aspect, showing the relation of the pericardium to the pulmonary vessels. *Ap.-Pc.Pl.* apicopectoral intersegmental plane; *Br.* main bronchus; *Br.u.* upper lobe bronchus; *H.F.Pl.* intersegmental plane in site of horizontal fissure; *I.P.V.* right inferior pulmonary vein; *I.P.V.* inferior pectoral vein; *Obl.F.* oblique fissure; *P.A.* division of pulmonary artery; *P.* pericardial recess. Other lettering as in Fig. 1.

ARTERIES

The right pulmonary artery (A. pulmonalis dextra) (Figs. 1–8)

Divisions

The right pulmonary artery is sometimes described as dividing into upper and lower divisions, of which the upper is the main supply of the upper lobe, while the lower supplies the middle and lower lobes. The upper division was described by Ewart

revived without acknowledgement by Peirce & Stocking, 1939). In the present account, Herrnheiser & Kubat's term *truncus superior* will be used, while the term *truncus inferior* will be used for their 'truncus intermedius' and its continuation the 'truncus inferior'. The so-called 'truncus intermedius' is short and of variable extent on account of differences in the origins of middle lobe arteries; its separate recognition seems to be an unnecessary complication for description.

The distinction of superior and inferior trunks is of value, since these two arteries are conspicuous features in the root of the lung and their respective distributions deserve separate consideration. The division of the right pulmonary artery into these two trunks takes place (Fig. 1) behind the right margin of the superior vena cava (Hovelacque *et al.* 1937; Brock, 1942).

Truncus superior (upper division, Fig. 1, *P.A.u.*). This artery enters the lung in front of the right bronchus at the level of the origin of the upper lobe bronchus. Its upper margin approximates to the level of the junction of the upper lobe bronchus with the main bronchus. It is covered in front by pleura except at its origin, where it lies behind the

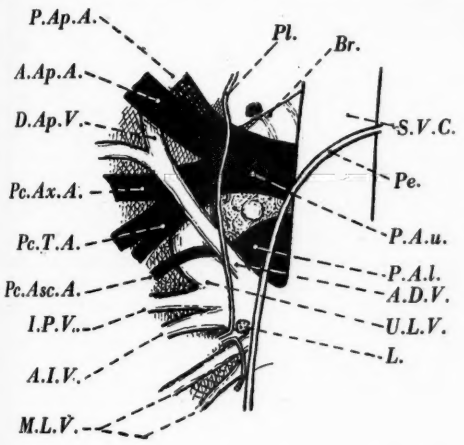


Fig. 3. Anterior exposure within hilum of right lung, showing relations of vessels. *A.I.V.* anterior interlobar vein; *D.Ap.V.* deep apical vein; *M.L.V.* middle lobe veins; *Pc.Asc.A.* pectoral ascending artery; *Pc.Ax.A.* pectoral axillary artery; *Pc.T.A.* pectoral terminal artery; *U.L.V.* great upper lobe vein. Other lettering as in Figs. 1 and 2.

superior vena cava. Lymph glands occupy the angle between the truncus superior and truncus inferior of the pulmonary artery. The truncus superior usually divides at once when it enters the lung. It is distributed to the apical segment and, in most lungs, to the greater part of the pectoral segment and a smaller portion of the posterior segment. Exceptionally (less than 10%) it supplies the whole of the upper lobe (p. 106).

Truncus inferior (lower division, Fig. 1, *P.A.l.*). This artery passes downwards and laterally into the lung and comes to lie between the upper lobe bronchus and the main bronchus. It is situated anteriorly in the root of the lung, below the upper division of the artery, but only a small triangular portion of the artery lies subjacent to the pleura of the lung root, above the superior pulmonary vein; below this level it is crossed in front by the superior pulmonary vein. Opposite the anterior lip of the lung in the hilum the anterior descending vein (Figs. 1, 2) joins the superior pulmonary vein in front of the artery. The medial part of the lower margin of the artery is overlapped in front by the pericardium enclosing a small pericardial recess (Fig. 2). The artery is not readily distinguishable from the superior pulmonary vein on anterior approach (as emphasized by Brock), on account of a strong fascial connexion between the pericardium and sheath of the pulmonary artery (Fig. 1). One or more lymph glands are placed in front of the artery and pericardial recess, above the vein.

Inferior to the artery is a pericardial recess that lies behind the superior pulmonary vein (Fig. 2). Posterior to it lies the commencement of the main bronchus for middle and lower lobes ('intermediate' bronchus of Ewart and of Peirce & Stocking).

On entering the lung the truncus inferior proceeds inferolaterally till it lies below the pectoral bronchus, from which it is separated by the great upper lobe vein and lymph glands (Figs. 3, 5). In this situation the lateral aspect of the artery comes to lie against the pleura in the depth of the interlobar fissure, immediately behind the junction of the oblique and horizontal fissures; lymph glands intervene (Fig. 4). The artery is at first in front of the main bronchus, but as this descends towards the lower lobe an increasingly large portion of the artery comes to lie laterally to it, and is here accessible from the posterior aspect of the root of the lung (Fig. 5), covered posteriorly by lymph glands.

The truncus inferior of the pulmonary artery ('truncus intermedius' of Herrnheiser & Kubat) supplies the middle and inferior lobes, and, in addition, it supplies a variable portion of the upper lobe, more especially its interlobar region (Figs. 6, 8 and 9); only exceptionally does it fail to give any artery to the upper lobe (two, or possibly three, lungs in fifty).

Upper lobe branch of the right pulmonary artery

In his description of the arteries Ewart discussed their relationship to the bronchi, and his account is therefore more suitable as a basis for the study of the relationship of vessels to the bronchopulmonary segments than the descriptions of later writers (Melnikoff, Herrnheiser and Kubat) who have largely neglected this aspect of their distribution. According to Ewart the greater part of the upper lobe is supplied by a pectori-apical trunk which has two branches, the 'pectoral' and 'ascending apical' distributed with branches of the 'pectoral' and 'apical' bronchi respectively. Ewart's 'apical' bronchus represents both the apical and posterior bronchi of subsequent accounts; the branch of his

'ascending apical' artery which is distributed with the bronchus now distinguished as the posterior bronchus appears to be his 'retro-apical' artery. This artery, according to him, may undertake the partial supply of the 'retro-axillary bronchial district', i.e. a part of the posterior bronchopulmonary

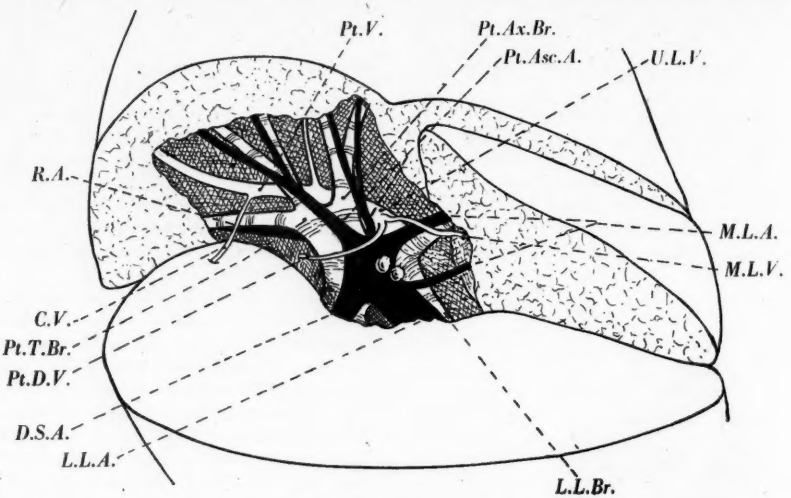


Fig. 4. Interlobar view of hilum of right lung (oblique fissure only), dissected. *C.V.* communicating vein between upper and lower lobe veins; *D.S.A.* artery to dorsal segment of lower lobe; *L.L.A.* lower lobe artery; *L.L.Br.* lower lobe bronchus; *M.L.A.* middle lobe arteries; *M.L.V.* a middle lobe vein; *Pt.Asc.A.* posterior ascending artery; *Pt.Ax.Br.* posterior axillary bronchus; *Pt.D.V.* posterior descending vein; *Pt.T.Br.* posterior terminal bronchus; *Pt.V.* deep vein from posterior segment; *R.A.* recurrent artery; *U.L.V.* great upper lobe vein.

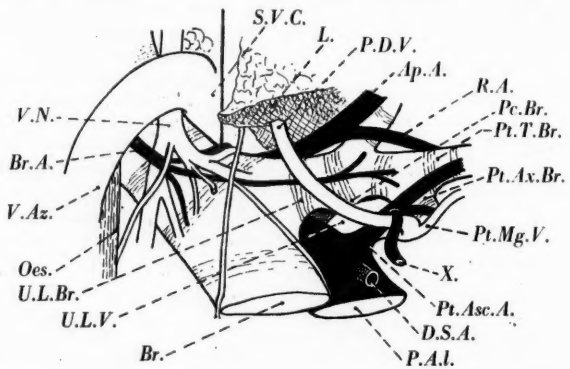


Fig. 5. Posterior exposure of vessels in root and hilum of right lung (upper lobe). *Ap.A.* apical artery; *Br.* bronchus of lower lobe; *Br.A.* bronchial artery; *D.S.A.* artery to dorsal segment of lower lobe; *L.* cut edge of lung; *Oes.* oesophagus; *P.A.l.* lower division of right pulmonary artery; *Pc.Br.* origin of pectoral bronchus; *P.D.V.* posterior descending vein; *Pt.Mg.V.* posterior marginal vein; *Pt.Asc.A.* posterior ascending artery; *Pt.Ax.Br.* posterior axillary bronchus; *Pt.T.Br.* posterior terminal bronchus; *R.A.* recurrent artery; *S.V.C.* superior vena cava; *U.L.Br.* upper lobe bronchus; *U.L.V.* great upper lobe vein; *V.Az.* vena azygos; *V.N.* vagus nerve; *X*, branch of posterior ascending artery to dorsal segment of lower lobe.

Ewart (p. 183) described an additional arterial supply to the upper lobe by an 'inferior axillary' artery, which is derived from the truncus inferior. segment, and it may even entirely supersede the 'retro-apical' artery.

Now there is general agreement in the literature

that the lower division (truncus inferior) of the pulmonary artery contributes to the arterial supply of the upper lobe. Fagan (1893) noted the occurrence of an artery to the upper lobe derived from the truncus inferior. Narath stated that arteries may thus enter the upper lobe from the truncus inferior, one, two or three in number. Hovelacque *et al.* have described such arteries by the names 'retrobronchial' and 'accessory lobar' (though under the latter name they do not exclude a distribution to the lower lobe). An arterial supply from the truncus inferior to the upper lobe appears from Melnikoff's scribed below (p. 108). Herrnheiser & Kubat have quoted Melnikoff for the occasional origin of an artery to the pectoral region (Ram. sterno-costalis descendens from the A. transversa interlobaris); this is identified as a 'pectoral ascending' artery of the present account. These authors have further noticed, in agreement with Felix (1930), an occasional small recurrent branch to the upper lobe from a branch of the middle lobe artery.

There are considerable differences in the descriptions of authors in regard to the branches to the upper lobe from the truncus superior of the pul-

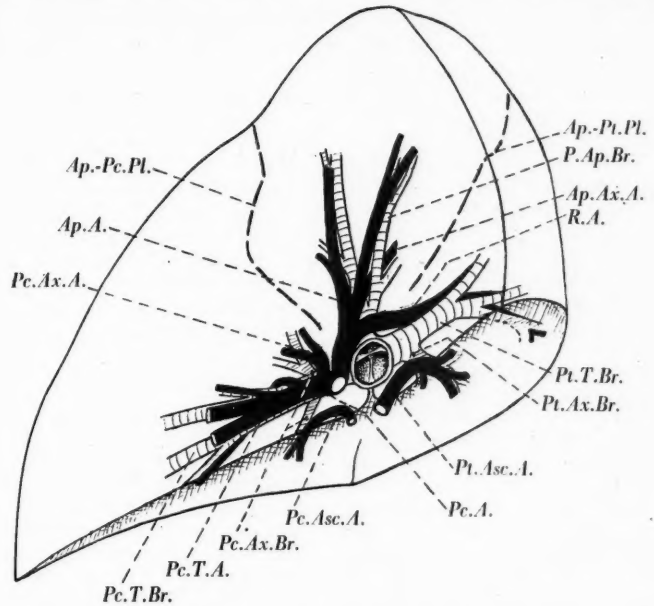


Fig. 6. Larger bronchi and arteries of upper lobe (a common pattern), medial aspect. *Ap.A.* apical artery; *Ap.Ax.A.* apical axillary artery; *Ap.-Pc.Pl.* apicopectoral intersegmental plane; *Ap.Pt.Pl.* apicoposterior intersegmental plane; *P.Ap.Br.* posterior apical bronchus; *Pc.A.* pectoral artery; *Pc.Asc.A.* pectoral ascending artery; *Pc.Ax.A.* pectoral axillary artery; *Pc.Ax.Br.* pectoral axillary bronchus; *Pc.T.A.* pectoral terminal artery; *Pc.T.Br.* pectoral terminal bronchus (lower branch); *Pt.Asc.A.* posterior ascending artery; *Pt.Ax.Br.* posterior axillary bronchus; *Pt.T.Br.* posterior terminal bronchus; *R.A.* recurrent artery.

account to be represented by his A. transversa interlobaris and probably also the A. ascendens accessoria, while Herrnheiser & Kubat described an A. axillaris which sometimes arises from the stem pulmonary artery and sometimes from the truncus superior (i.e. the main upper lobe artery); the former variety, but not the latter one, can be identified with the 'inferior axillary artery' of Ewart. They have also mentioned that small arterial branches are sometimes found below the pectoral bronchus, but do not state their origin whether from the truncus superior or truncus inferior; they may be represented by the pectoral ascending artery de-

monary artery. Herrnheiser & Kubat have recognized Ewart's two arteries, 'pectoral' and 'ascending apical' in their A. pectoralis and A. apicalis, and these authors have further identified them with those named truncus horizontalis and truncus ascendens by Backman (whose original paper it has not been possible to consult). Felix differs from other authors in describing the pectoral (his 'ventral' artery) as arising usually from the main stem (i.e. truncus inferior) independently of the apical artery. Melnikoff's account differs from other authors inasmuch as he names five arteries from the truncus superior, of which one is the apical artery

and the other four, as pointed out by Herrnheiser & Kubat, may be identified with various branches of the pectoral artery.

The arterial supply to the posterior part of the upper lobe has been the subject of considerable divergences in description, and correlation of the various accounts is difficult, because, apart from Ewart, the relation of arteries to bronchi has generally been disregarded. From Ewart's description it appears that the posterior bronchopulmonary segment is supplied by two arteries, viz. the retro-apical and the inferior axillary, which vary reciprocally in their respective contributions. Subsequent authors have not improved on the account. Herrnheiser & Kubat's axillary artery is evidently, from their account, distributed to a part of the posterior segment. They allow it a great diversity of origin and define it by reference to its distribution in the lung. It is said to arise usually from the stem pulmonary artery (i.e. truncus inferior), and when this is so it evidently represents Ewart's inferior axillary artery. But Herrnheiser & Kubat claimed the same name for an artery arising from the apical or even from the pectoral artery, i.e. from branches of the truncus superior. They also describe a ramus costalis of the apical artery which appears to contribute to the posterior segment; they identify it with Melnikoff's ramus costo-vertebralis of the apical artery. It appears from these accounts that there are considerable variations in the manner in which the truncus superior of the pulmonary artery contributes the arterial supply of the posterior bronchopulmonary segment, and further, that this segment is also commonly supplied by one or more branches of the inferior division of the artery.

In the following account, based on the present series of fifty lungs, the pectoral artery corresponds with that so named by previous authors. The apical artery corresponds also, except that previous authors generally have described the recurrent artery of this description as a branch of the apical artery. The ascending arteries of this account correspond to the arteries which reach the upper lobe from the truncus inferior of the pulmonary artery or from one of its branches.

Branches of right pulmonary artery to the right upper lobe (Figs. 6, 9, 14 and 15)

	Branches	% frequency in 50 lungs
Truncus superior	R. pectoralis	94
	R. apicalis	100
	R. recurrens	58
Truncus inferior	R. ascendens pectoralis	48
	R. ascendens posterior	78
	R. ascendens from middle lobe artery	6

Branches of the truncus superior ('upper division' or 'first branch') of the right pulmonary artery

The truncus superior of the pulmonary artery divides into branches immediately it passes the pleural reflexion from root to lung. In the majority of lungs it provides three arteries, which will be named pectoral, apical and recurrent (Figs. 6, 7). These give rise to branches that accompany bronchi within the pectoral, apical and posterior segments respectively. Their precise manner of origin shows much individual variation (Fig. 7). The pectoral and recurrent arteries are not constantly present, the latter being absent in 42 %, the former only seldom absent (viz. in 6 %).

The pattern of branching of the truncus superior

The truncus superior shows much variation (as pointed out by Ewart and subsequent authors) in the manner in which arteries arise from it. The appearances presented on examination of the hilum of the lung vary considerably in consequence. The differences are in the main dependent on (1) the presence or absence of a recurrent artery, (2) immediate or late division of the apical artery or of the pectoral artery. The various types have been classified primarily with reference to the differences of arterial pattern presented within the hilum of the lung.

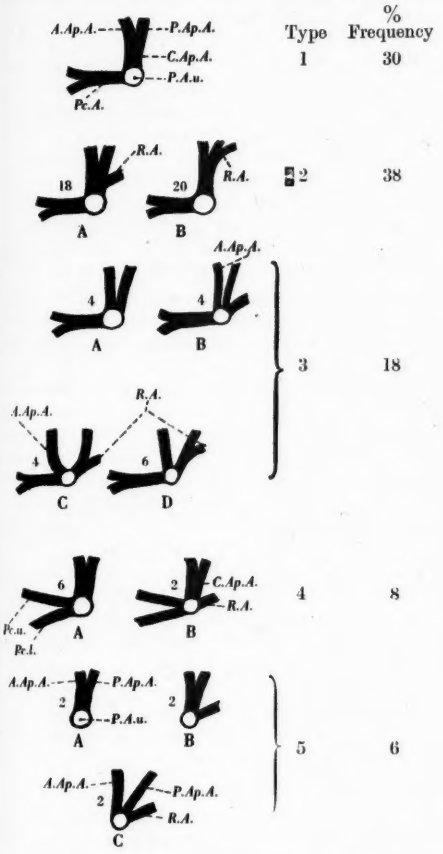
In 30 % of lungs (type 1) the truncus superior divides into two branches, the pectoral and apical. In a further 38 % (type 2) the pattern is the same except that a recurrent artery arises either from the

Arterial nomenclature

Ewart	Pectori-apical trunk	Pectoral A.	Ascending apical A.	Retro-apical A.	Inferior or pulmonary axillary A.
Melnikoff	—	Four branches named separately	A. apicalis *seu* ascendens	Ramus costovertebralis of A. ascendens	A. transvers interlobaris
Hovelacque	Artère principale du lobe supérieur	—	—	—	A. rétrobronchique
Herrnheiser & Kubat	Truncus superior	A. pectoralis	A. apicalis	Ramus costalis of A. apicalis	A. axillaris (in some instances)
Appleton	Truncus superior	A. pectoralis	A. apicalis	A. recurrens	A. ascendens posterior

(common) apical or the posterior apical artery. Types 1 and 2 account for two-thirds of all lungs.

In 18 % (type 3) the anterior and posterior terminal apical arteries (accompanying corresponding bronchi) arise independently from the truncus



Type	% Frequency
1	30
2	38
3	18
4	8
5	6

Fig. 7. Scheme of variations of branching of upper division of right pulmonary artery in fifty lungs, showing percentage frequencies (from medial aspect). *A.Ap.A.* anterior apical artery; *C.Ap.A.* common apical artery; *P.A.u.* upper division of pulmonary artery; *P.Ap.A.* posterior apical artery; *Pc.A.* pectoral artery; *Pc.l.* pectoral terminal artery, lower branch; *Pc.u.* pectoral terminal artery, upper branch; *R.A.* recurrent artery.

superior, with variants that depend on connexions at the sites of origin with the pectoral or recurrent arteries (Figs. 7, 8).

In 8 % (type 4) respectively the upper and lower terminal pectoral arteries arise separately from the truncus superior, with or without a recurrent artery.

In 6 % (type 5) there was no pectoral artery.

A more detailed classification of types, with frequencies, is shown in Fig. 7.

It may be observed, in reference to the identification of branches of the truncus superior at the root of the lung, that there are two main branches in types 1, 2B, 5B (52 %); there are three in types 2A, 3A, 3C, 3D, 4A, 5C (40 %), and four in types 3B, 4B (6 %). In type 5A the branching of the artery takes place within the lung at some distance from its root.

Herrnheiser & Kubat's 'thamnoid' type corresponds approximately to the types here described with three or four branches; their 'dendroid' type represents the other types now described.

The different appearances presented on anterior approach to the root of the lung are discussed below (p. 116).

The pectoral artery (Figs. 1–3) is readily seen on anterior approach to the root when the pleura is divided where it passes on to the lung. At the margin of the lung it is generally crossed by the anterior descending vein, a tributary of the superior pulmonary vein, which shows great variation in size. Entering the lung, the artery turns forwards close to the mediastinal surface, generally directed somewhat downwards (though occasionally inclined a little upwards, especially when there is no horizontal fissure). The artery separates the pectoral bronchus from the mediastinal surface of the lung.

Lymph glands lie below the first inch of the artery, separating it from the great upper lobe vein and the pleura of the interlobar fissure. The artery was absent in 6 % of the lungs examined.

Distribution

The pectoral artery commonly divides into 'pectoral axillary' and 'pectoral terminal' branches close to its origin.

(1) The ramus pectoralis axillaris (represented by the 'oblique' branches of Melnikoff, the 'costopectoral' branches of Herrnheiser & Kubat) arises from the pectoral artery, generally near to the origin of the latter artery. It was absent in 4 % of the lungs that possessed a pectoral artery. It passes laterally above the pectoral bronchus, close to the origin from the latter of the pectoral axillary bronchus. In 42 % of lungs it divides into upper and lower branches, termed 'costal' and 'interlobar' respectively, which accompany the corresponding bronchi of the pectoral axillary subsegment. In 58 % of lungs this artery fails to supply some part of the pectoral axillary system of bronchi, its place being then taken in part by a pectoral ascending artery which is derived from the truncus inferior and supplies the region nearest the interlobar surface.

The inferior or interlobar branch, when present, runs towards the interlobar surface by passing to the lateral side of the pectoral bronchus. The superior or costal branch often has a posteriorly

directed branch, which is distributed with a corresponding branch of the pectoral axillary bronchus; in 14% of lungs this posterior branch contributed to the supply of the adjacent part of the apical segment; in 8% of lungs it was large and passed backwards on the lateral side of the base of the apical bronchus (Figs. 14A, 15B) to supply a part or the whole of the posterior bronchopulmonary segment.

The ramus pectoralis terminalis passes forwards in most lungs on the medial aspect of the pectoral bronchus. It usually divides, after a course of about one inch, into superior and inferior branches (the sternopectoral arteries of Herrnheiser & Kubat), close to the corresponding division of the bronchus. Occasionally the bifurcations of the bronchus and artery are found very close to the hilum of the lung. At some point along the course of the pectoral

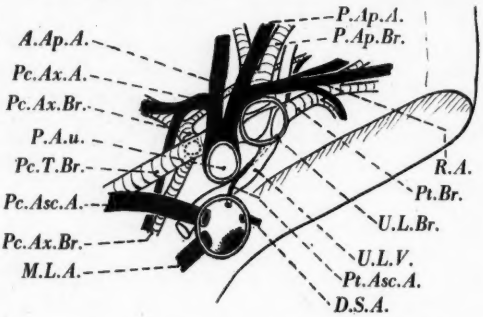


Fig. 8. Hilum of upper lobe of a right lung, relations of vessels (from the medial aspect) illustrating unusual arterial supply to the pectoral segment. *D.S.A.* artery to dorsal segment of lower lobe; *M.L.A.* middle lobe artery; *P.Ap.Br.* posterior apical bronchus; *Pc.Asc.A.* pectoral ascending artery; *Pc.Ax.A.* pectoral axillary artery arising from anterior apical artery; *Pc.Ax.Br.* pectoral axillary bronchus, upper and lower branches; *Pc.T.Br.* pectoral terminal bronchus; *Pt.Br.* posterior bronchus; *Pt.Asc.A.* posteriorly situated subsidiary pectoral ascending artery; *R.A.* recurrent artery; *U.L.Br.* upper lobe bronchus; *U.L.V.* great upper lobe vein. Other lettering as in Fig. 1.

terminal artery or of one of its branches, an interlobar branch passes laterally above the pectoral bronchus and accompanies a corresponding interlobar branch of the bronchus.

This artery supplied the whole of the pectoral terminal subsegment in 44% of the present series; in the majority of the other lungs it supplied the greater part of the segment, the remaining portion receiving branches of the pectoral ascending artery. Variations in the distribution of the pectoral artery and in the supply of the pectoral bronchopulmonary segment are illustrated in Fig. 14.

The apical artery (Figs. 1, 2 and 7) is readily seen on anterior approach to the root when the pleura is divided where it passes into the lung. It passes obliquely upwards and laterally on the medial aspect of the apical bronchus, receding gradually from its mediastinal surface. It divides either at once or after a short or long course into anterior and posterior apical arteries that accompany the corresponding bronchi. It also provides an apical axillary artery distributed with the axillary branch of the apical bronchus (Fig. 6); this artery arises either from the main apical artery or from one of its terminal branches. In 20% of lungs the anterior and posterior branches arose separately from the upper division of the pulmonary artery and not by a common apical arterial stem (Figs. 7, 8). In 48% of lungs the recurrent artery arises as a branch of the common apical or the posterior apical artery.

The apical artery occasionally assists in the supply of adjacent segments. It contributed a branch to the pectoral segment in 4%, and in 4% of lungs it gave a branch to the posterior segment which was additional to a recurrent artery supplying that segment (Fig. 13).

The recurrent artery (Figs. 5–8, 18, 19), when present, is derived from the truncus superior of the right pulmonary artery or from the apical artery or posterior apical artery. It generally passes backwards immediately above the upper lobe bronchus, and it is thus concealed from view by the truncus superior when an anterior approach is made to the root of the lung. It was absent in 42% of the lungs examined. When present it did not often supply the whole of the posterior segment, viz. in 18% of all right lungs.

The part of the posterior segment (Figs. 6, 8) supplied by the recurrent artery includes the whole or a part of the terminal subsegment, the whole or a part of the axillary subsegment or parts of each of these subsegments.

Variations in the distribution of the recurrent artery and the supply of the posterior segment are shown in Figs. 9 and 15.

Branches of the truncus inferior, or lower division of the right pulmonary artery

Branches from the truncus inferior have been found supplying some part of the upper lobe of the right lung (Figs. 6, 8 and 9) in the overwhelming majority of lungs examined, viz. in some 95% (forty-seven lungs out of fifty, with one doubtful instance). In twenty-eight lungs there was one such artery, in seventeen there were two, and in three there were three. These arteries will be distinguished as 'ascending' arteries.

In addition, three instances of an ascending artery from a middle lobe artery have been seen; they supplied a part of either the pectoral or the posterior segment (Figs. 9K, 19).

Every part of the interlobar region of the upper lobe has been found supplied by an ascending artery

or arteries from the truncus inferior in some example or another. An approximate classification of these arteries may be made according to whether it is the pectoral or posterior segment which is thus supplied,

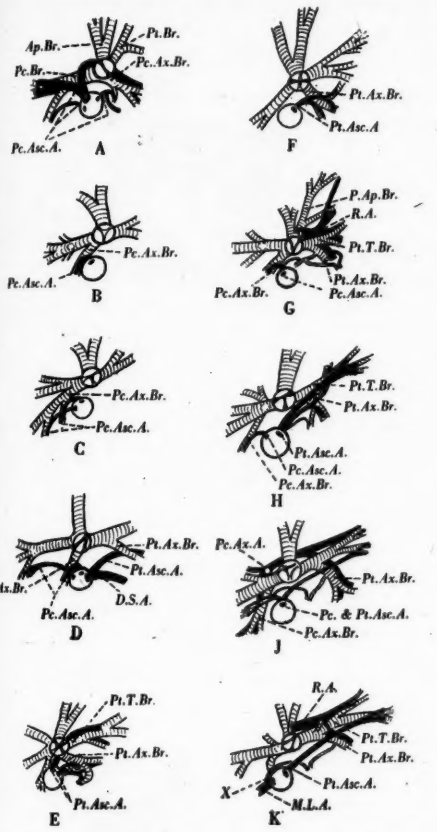


Fig. 9. Principal variations of ascending arteries from the lower division of the right pulmonary artery distributed to the upper lobe, together with the associated patterns of the bronchi (arteries in black). *Ap.Br.* apical bronchus; *D.S.A.* artery to dorsal segment of lower lobe; *M.L.A.* middle lobe artery; *Pc.Asc.A.* pectoral ascending arteries; *Pc.Ax.A.* pectoral axillary artery; *Pc.Ax.Br.* pectoral axillary bronchus; *P.Ap.Br.* posterior apical bronchus; *Pt.Asc.A.* posterior ascending arteries; *Pt.Ax.Br.* posterior axillary bronchus; *Pt.Br.* posterior bronchus; *Pt.T.Br.* posterior terminal bronchus; *R.A.* recurrent artery; *X*, ascending artery from middle lobe artery; *Pc.Br.* pectoral bronchus.

the arteries being distinguished as 'pectoral ascending' or 'posterior ascending' respectively. These arteries, with only occasional exceptions, differ also in the site of their origin on the truncus inferior, and in their relation to the great upper lobe vein. Of the two, the pectoral ascending artery arises the more medially, just within the hilum of the lung on the anterosuperior aspect of the truncus inferior, while the posterior ascending artery arises about an inch within the lung on its posterosuperior aspect. A pectoral ascending artery passes to the medial side of and above the great upper lobe vein to reach the pectoral segment (Figs. 8, 9); a posterior ascending artery takes origin below and behind that vein and then pursues a course which takes it posteriorly or posterolaterally away from that vein (Figs. 5, 23, 26).

Occasionally a common arterial stem divides into pectoral and posterior ascending arteries (Figs. 9 G, J, 10); it arises from the middle of the superior aspect of the truncus inferior, i.e. in a position intermediate between the normal sites of origin of these arteries. In one instance an artery distributed in

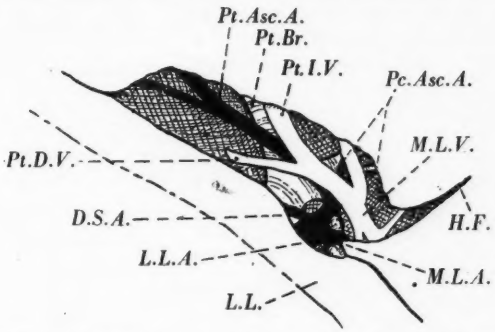


Fig. 10. Interlobar view of hilum of right lung through oblique fissure (venous type, p. 119). *H.F.* horizontal fissure; *L.L.* upper lobe; *L.L.A.* lower lobe artery; *M.L.A.* middle lobe artery; *M.L.V.* middle lobe veins; *Pt.I.V.* posterior interlobar veins; *Pt.D.V.* posterior descending vein. Other lettering as in Fig. 8.

the posterior axillary subsegment and therefore by our definition a posterior ascending artery, took origin anterosuperiorly on the truncus inferior and passed backwards medially to the great upper lobe vein, below it and the junction of the upper lobe bronchus with the main bronchus.

Either the pectoral or posterior ascending artery may divide almost at once into two that accompany different subsidiary bronchi; and either of them may be represented by *two* arteries that arise independently from the main lower division, i.e. there may be two pectoral ascending arteries or two posterior ones (Figs. 4, 8, 9C, D). A posterior ascending artery sometimes shares an origin with the artery of the dorsal segment of the lower lobe; its origin is in any case usually close to the latter artery (Figs. 5, 10 and 12). An instance of three separate pectoral ascending arteries has been encountered (Fig. 9A).

The principal varieties that have been encountered in a series of fifty lungs are shown in Fig. 9A–K, together with the associated patterns of the larger bronchi; the latter illustrate some of the principal variations of the bronchi.

The commonest pattern of the ascending arteries is one in which the posterior ascending artery is alone present; rather less often there are both posterior and pectoral ascending arteries, arising far apart on the upper aspect of the lower division of the pulmonary artery (Figs. 6, 8 and 9D). The posterior ascending artery commonly divides into two branches, destined respectively for the posterior axillary and posterior terminal subsegments, while the pectoral ascending artery is distributed to the lower part of the pectoral axillary subsegment.

Either the pectoral ascending or the posterior ascending artery may be very large or minute, with a distribution of corresponding extent (compare Figs. 9A, B, G, H).

Variations in the number of the ascending arteries are set out below:

Groups:	No. of lungs
1. Pect. asc. artery but no post. asc. artery	5
2. Post. asc. artery but no pect. asc. artery	23
3. Pectoral and posterior ascending arteries	13
4. Two posterior ascending arteries	1
5. Two pectoral ascending arteries	3
6. Three ascending arteries	3
7. No ascending arteries	2
	50
Common stem for posterior ascending artery and artery to dorsal segment of lower lobe	3
Ascending artery from middle lobe artery	3 (all in group 2)
Common stem for anterior and posterior ascending arteries	4 (all in group 3)
Anterior ascending artery entirely replaces pectoral artery	2

Arteria pectoralis ascendens (Figs. 3, 10). This artery was present in 48 % of lungs. Its origin is concealed, on anterior approach, by the anterior descending vein (Fig. 3). It arches over the great upper lobe vein below the level of the pectoral artery and bronchus, from which it is separated by lymph glands. In one instance out of the twenty-four lungs exhibiting pectoral ascending arteries, the artery passed to the lateral side of the vein and was concealed on interlobar approach merely by superficial interlobar veins (Fig. 10). The great upper lobe vein generally separates it from the pleura in the depth of the interlobar fissure and it is difficult to see this artery on interlobar approach.

The pectoral ascending artery supplies the interlobar region of either the terminal or axillary subsegment of the pectoral bronchopulmonary segment or, more commonly, parts of both segments (Fig. 13). It may be represented by two arteries

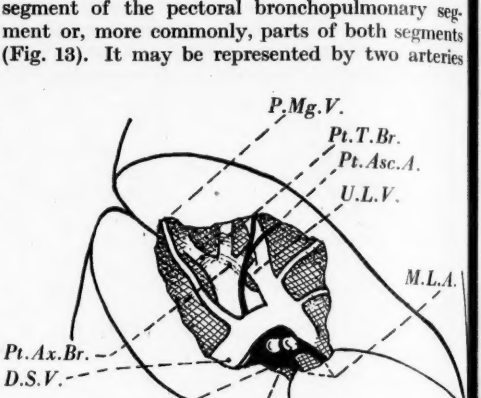


Fig. 11. Interlobar view of hilum of right lung through oblique and horizontal fissures (venous type, p. 119). *D.S.V.* vein from dorsal segment of lower lobe; *L.* lymph glands; *L.L.A.* lower lobe artery; *P.Mg.V.* posterior marginal vein; *Pt.Ax.Br.* posterior axillary bronchus; *Pt.T.Br.* posterior terminal bronchus. Other lettering as in Fig. 8.

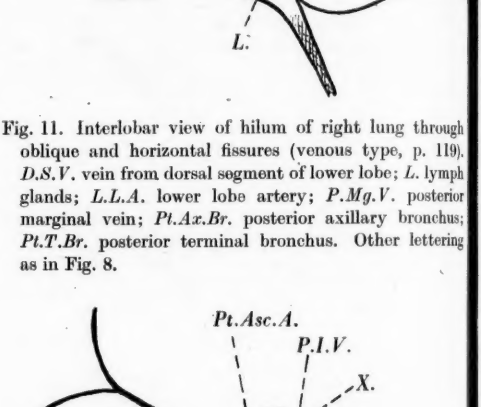


Fig. 12. Interlobar view of hilum of right lung through oblique fissure, showing ascending artery from middle lobe artery. *L.L.A.* lower lobe artery; *P.I.V.* posterior interlobar vein; *X*, ascending artery to posterior axillary subsegment from middle lobe artery. Other lettering as in Fig. 8.

with separate origins from the truncus inferior (Fig. 9C, D); sometimes a single stem artery has two considerable branches distributed to different parts

of the pectoral segment. Variations in its distribution are illustrated in Figs. 9, 14. Occasionally this artery is large and supplies the greater part or even the whole (6 %) of the pectoral bronchopulmonary segment. An appearance is then produced of a 'pectoral artery' arising from the lower division instead of from the upper division of the pulmonary artery (Figs. 9A, 14E).

Occasionally, as stated above, a pectoral ascending artery arises by a common stem with a posterior ascending artery (Figs. 9J, 10).

The posterior ascending artery (the 'retrobronchial' of Hovelacque) was present in 78 % of lungs (Figs. 4, 5, 8, 12, 13, 23 and 24). It arises from the posterosuperior aspect of the truncus inferior where this vessel turns downwards some ¾ inch from its commencement. At its origin it is below the pectoral bronchus from which it is separated by lymph glands. On posterior approach the origin of the artery is found well within the lung concealed by lymph glands just above the origin of the main artery to the dorsal segment of the lower lobe (Fig. 5). Exceptionally (6 %) it was found to share a common origin with the artery of the dorsal segment (Nelson, 1932) of the lower lobe (Fig. 9A). On the other hand, the posterior ascending artery may contribute a small artery to a part only of the dorsal segment of the lower lobe (Fig. 5).

On interlobar approach this artery is generally a conspicuous feature (Figs. 4, 12) passing upwards from the inferior division of the pulmonary artery, though it is sometimes concealed by a large vein which joins the great upper lobe vein, either from the upper lobe (a posterior descending vein, Fig. 25) or from the lower lobe (Fig. 11, *D.S.V.*, a communicating vein).

As stated above, this artery is not infrequently represented by two arteries which arise separately from the inferior division.

A posterior ascending artery occasionally has a common origin with a pectoral ascending artery (Figs. 9J, 10), the two vessels then supplying adjacent axillary subsegments (pectoral and posterior).

The posterior ascending artery varies greatly in size, since it may supply only a small pulmonary lobule adjacent to the hilum (Fig. 9G), or it may (32 %), on the other hand, supply the whole posterior bronchopulmonary segment (Fig. 9H). Kent & Blades (1942) have claimed that ligature of this artery is of no consequence. This cannot be accepted in respect of those not infrequent instances in which it supplies the greater part or even the whole of the posterior segment, unless it is accepted also for any other large artery supplying the upper lobe.

With few exceptions the posterior ascending artery, when present, supplies some part or the whole of the posterior axillary subsegment. In addition it often supplies a part or the whole of the terminal subsegment.

The detailed distribution of the posterior ascending artery, with the bronchi of the posterior segment, is set out below:

Bronchi of posterior segment

	No. of lungs
Axillary + terminal	18
Axillary + inferior terminal	3
Axillary only	6
Axillary anterior branch + inferior terminal	3
Axillary costal branch + terminal	1
Axillary anterior branch	4
Axillary costal branch	1
Terminal only	2
Superior terminal (posterior branch) + inferior terminal	1
None	11
	50

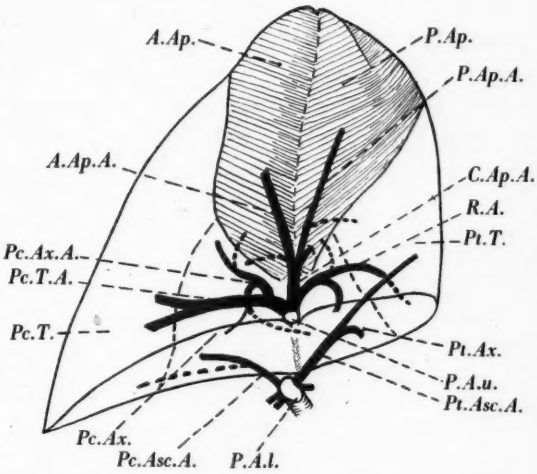


Fig. 13. Scheme of arterial supply to the main segments and subsegments of the upper lobe of the right lung. (Interrupted lines show less usual branches.) **Subsegments:** *Pc.Ax.* pectoral axillary; *Pc.T.* pectoral terminal; *A.Ap.* anterior apical; *P.Ap.* posterior apical; *Pt.Ax.* posterior axillary; *Pt.T.* posterior terminal. **Arteries:** *Pc.Asc.A.* pectoral ascending; *Pc.Ax.A.* pectoral axillary; *Pc.T.A.* pectoral terminal; *C.Ap.A.* common apical; *A.Ap.A.* anterior apical; *P.A.u.* upper division of right pulmonary; *P.A.l.* lower division of right pulmonary; *P.Ap.A.* posterior apical; *R.A.* recurrent; *Pt.Asc.A.* posterior ascending.

Ascending arteries from the middle lobe artery. A small artery supplying bronchi near the interlobar surface of the upper lobe was found in three lungs (6 %) arising from the middle lobe artery (Figs. 9K, 12). In two instances it supplied a part of the pectoral axillary subsegment, in one instance a part of the posterior axillary subsegment.

The arterial supply of the bronchopulmonary segments of the right upper lobe

The distribution of the arteries enumerated in the previous section will be reviewed with reference to the supply of the various segments of the upper lobe. The general scheme is shown in Fig. 13. No

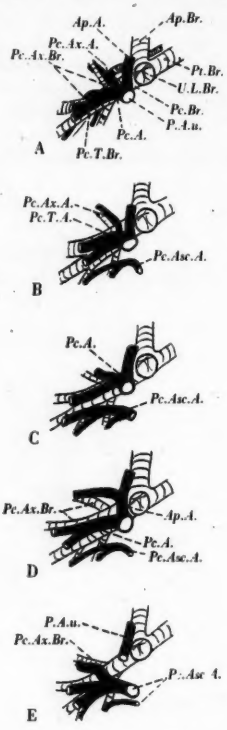


Fig. 14. Scheme of arterial supply of the pectoral segment, showing principal variations (medial aspect). The commonest type shown in B. **Bronchi:** *Ap.Br.* apical bronchus; *Pc.Br.* pectoral; *Pc.Ax.Br.* pectoral axillary; *Pc.T.Br.* pectoral terminal; *Pt.Br.* posterior bronchus; *U.L.Br.* upper lobe bronchus. **Arteries:** *Ap.A.* apical artery; *P.A.u.* pulmonary artery, upper division; *Pc.A.* pectoral from upper division of pulmonary artery; *Pc.Asc.A.* pectoral ascending, from lower division of pulmonary artery; *Pc.Ax.A.* pectoral axillary; *Pc.T.A.* pectoral terminal artery.

example was encountered in this series of fifty lungs of any exceptional supply from systemic arteries as described by East & Barnard (1938), Ingalls (1932), Menke (1936) and others.

Pectoral segment (Fig. 14). The pectoral segment almost always receives its main arterial supply by the pectoral branch of the upper division of the right pulmonary artery. In addition it often receives a pectoral ascending artery from the lower division of the right pulmonary artery, which is distributed to the lower bronchi of the terminal or of the axillary subsegment or of both (Fig. 14B).

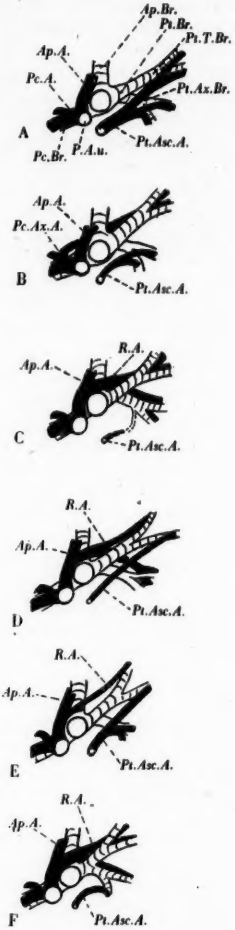


Fig. 15. Scheme of arterial supply of the posterior segment, showing principal variations (medial aspect). All types except B are common. **Bronchi:** *Ap.Br.* apical; *Pt.Br.* posterior; *Pt.Ax.Br.* posterior axillary; *Pt.T.Br.* posterior terminal; *Pc.Br.* pectoral. **Arteries:** *P.A.u.* upper division of pulmonary artery; *Ap.A.* apical; *Pc.A.* pectoral; *Pc.Ax.A.* pectoral axillary; *Pt.Asc.A.* posterior ascending from lower division of pulmonary artery; *R.A.* recurrent.

Only exceptionally is the whole of the pectoral segment (Fig. 14E) supplied by a pectoral ascending artery or arteries.

The part of the segment adjacent to the apical

segment is occasionally supplied by a branch of the apical artery (Fig. 14D) and the part adjacent to the horizontal fissure occasionally receives an artery from the middle lobe artery (i.e. from the inferior division of the pulmonary artery).

The posterior segment (Fig. 15). The posterior segment has a very varied arterial supply. Usually it is supplied by the posterior ascending artery from the lower division of the pulmonary artery, but in about one-third of all lungs examined the segment is supplied both by this artery and by the recurrent artery from the upper division, while in about one-fifth of all lungs the latter is the sole supply of the posterior segment.

Either the axillary or the terminal subsegment may receive an arterial supply from the recurrent artery and either may receive an arterial supply from the posterior ascending artery (Fig. 15 D, E, F).

Detailed arterial supplies of bronchopulmonary segments (in fifty lungs)

		Frequency	Division of pulmonary artery*
Pectoral segment:	Pectoral artery only	44	U
	Pectoral + pectoral ascending	42	U + L
	Pectoral + branch of middle lobe artery	4	U + L
	Pectoral ascending only	6	L
	Pectoral + apical	4	U
Apical segment:	Apical artery only	70	U
	Apical + pectoral	14	U
	Apical + recurrent	16	U
Posterior segment:	Posterior ascending only	32	L
	Posterior ascending + recurrent	32	U + L
	Recurrent only	22	U
	Pectoral only	2	U
	Pectoral + posterior ascending	4	U + L
	Pectoral + posterior ascending + recurrent	2	U + L
	Apical + posterior ascending	4	U + L
	Middle lobe artery + posterior ascending + recurrent	2	U + L

* U = upper division (truncus superior); L = lower division (truncus inferior).

Exceptionally the axillary branch of the pectoral artery supplies a part of the posterior segment, generally its lower part (Fig. 15B). The part of the segment adjacent to the apical segment occasionally receives an artery from the apical artery (Fig. 13), and the part near the junction of the oblique and horizontal fissures exceptionally receives a branch from the middle lobe artery (Figs. 9K, 12, 19).

The apical segment. This receives its main arterial supply from the apical artery, a branch of the upper division of the pulmonary artery. Not uncommonly the part adjacent to the pectoral segment (i.e. just below the subclavian groove) is supplied by a branch of the pectoral artery; the posterior part of the segment is sometimes supplied by a branch of the recurrent artery (Fig. 13). No instance has been encountered in which any part of the segment is supplied by a branch of the lower division of the pulmonary artery.

PULMONARY VENOUS DRAINAGE

In all of the fifty right lungs examined, the right superior pulmonary vein was the main drainage route for both middle and upper lobes, as stated by Ewart, Hovelacque *et al.* and Melnikoff. Additional means of drainage were found in a considerable number of the lungs.

Communicating veins invariably cross the junctional zones when, as is so frequently found, there is an incomplete separation of the upper from the middle lobe or from the lower lobe. These either drain a part of the upper lobe into veins of the middle or lower lobe, or vice versa. Even when a nearly complete fissure is present it is not unusual, as pointed out by Herrnheiser and Kubat, for a single venous stem to receive blood from the adjacent interlobar surfaces of the upper and middle lobes. A large communicating vein is not infrequently found to pass between the upper and lower lobes near the mediastinal surface behind the lung root; it conveys blood sometimes in one direction, sometimes in the other. It is doubtless a very large vein of this kind that has been described by Hovelacque as a right superior pulmonary vein, passing behind the root of the lung. Hyrtl (1837), MacCready (1918), Cleland (1941) and others have described instances of drainage of pulmonary veins into the systemic venous system; no such instance was found in the present series.

The right superior pulmonary vein (V. pulmonalis dextra superior)

The right superior pulmonary vein (Figs. 2, 3) is formed by the union of veins from the middle and upper lobes in the hilum of the lung, in front of the

lower division of the pulmonary artery. It proceeds medially in the root of the lung with a slight downward inclination and on entering the pericardium is almost entirely below the level of the artery. A pericardial pocket separates the vein from the posteromedial angle of the middle lobe.

The superior pulmonary vein generally receives two large veins from the upper lobe (Figs. 1, 3):

(1) The anterior descending vein (V. subpleuromediastinalis of Herrnheiser and Kubat; the superficial inner ascending trunk of Ewart), which joins its upper aspect at the reflexion of the pleura on to it from the lung.

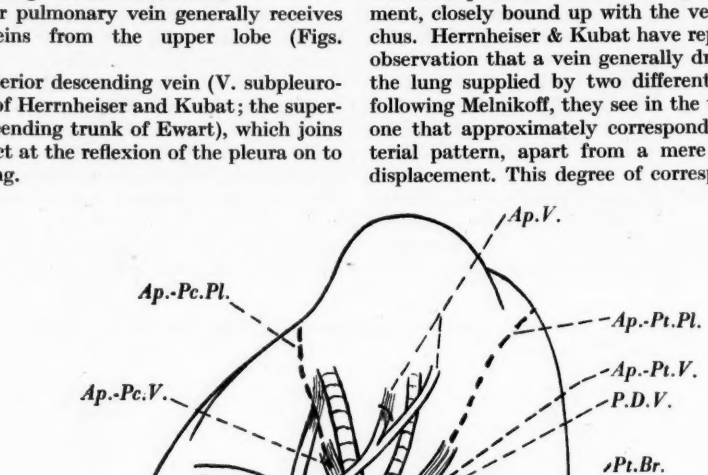


Fig. 16. Scheme of usual pattern (type) of venous drainage of upper lobe of right lung (deep veins shaded). *S.P.V.* superior pulmonary vein. **Intersegmental planes:** *Ap.-Pc.Pl.* apicopectoral; *Ap.-Pt.Pl.* apicoposterior. **Superficial veins:** *A.D.V.* anterior descending; *A.I.V.* anterior interlobar; *I.P.V.* inferior pectoral; *M.I.V.* middle interlobar; *P.D.V.* posterior descending; *Pt.Mg.V.* posterior marginal; *Ap.V.* apical. **Deep veins:** *U.L.V.* great upper lobe vein; *Ap.-Pc.V.* apicopectoral; *Ap.Pt.V.* apicoposterior; *Ap.V.* apical; *Pt.V.* posterior. **Bronchi:** lettering as in Fig. 14.

(2) The great upper lobe vein (Ramus posterior of Melnikoff), which joins its posterolateral aspect, after passing under the lateral end of the upper lobe bronchus.

Other veins from the upper lobe are more variable and are detailed below (pp. 113, 114, Fig. 16).

General arrangement of the veins of the upper lobe

The significance of the fundamental relationship of veins to the bronchopulmonary segments and intersegmental planes, to which attention has been drawn above (p. 97) has been inadequately recognized in the German accounts of the veins of the lungs. The pattern of the veins is indeed, as pointed out by Ewart, radically different from that of the arteries, since they run in the planes between segments and subsegments, whereas an artery occupies a central position within the segment or subsegment, closely bound up with the ventilating bronchus. Herrnheiser & Kubat have repeated Ewart's observation that a vein generally drains regions of the lung supplied by two different arteries, but, following Melnikoff, they see in the venous pattern one that approximately corresponds with the arterial pattern, apart from a mere topographical displacement. This degree of correspondence finds expression in the nomenclature of these authors, which ignores the distinctive character of the venous pattern. It is desirable that the specific relations of veins to the accepted pattern of bronchopulmonary segments should find recognition in the names which are used. In the following account, accordingly, the veins which lie between segments will be named with reference to the planes in which they lie. Their tributaries which lie in the subsegmental planes within the segments will be named after the segments.

The veins of the lungs fall into two categories from the point of view of topography, the **superficial** and the **deep**. Superficial ones run close to the

pleural surfaces and drain the exposed parts of the segments: deep ones lie in intersegmental planes and drain adjacent segments. When a fissure is absent or incomplete veins of the superficial series lie between segments belonging to different lobes and, like the deep ones, receive tributaries from adjacent segments. The larger veins of the pectoral segment are mainly superficial, on its mediastinal and interlobar surfaces. The apical and posterior segments tend, however, to drain by deep veins (Figs. 16, 21 A and 23); less often their chief drainage is by superficial veins on their mediastinal and interlobar surfaces (Figs. 17, 21 B). Thus the larger collecting veins consist of a superficial and a deep series of which the superficial ones are most constant in the anterior parts of the mediastinal and interlobar surfaces.

The smaller veins from the costal region of the upper lobe dive into the lung and join the deep veins, just as those of the posterior parts of the mediastinal and interlobar surfaces commonly do.

The chief collecting sites for deep veins within the upper lobe are in the planes between the bronchopulmonary segments, apicopectoral and apicoposterior respectively (Figs. 13, 16). Large veins in these planes, which will be named the apicopectoral and apicoposterior veins respectively, drain the adjacent bronchopulmonary segments, and these planes can be opened up only by severance of the tributaries on one side or other of the plane. The veins generally unite close to the lateral end of the upper lobe bronchus to form the great upper lobe vein, the largest tributary of the right superior pulmonary vein.

Variations of the venous pattern depend primarily on the enlargement or reduction of alternative routes by which blood can leave the segments.

Differences of this kind are illustrated in the two types of venous pattern figured by Melnikoff.

Deep veins (Fig. 16)

V. apicopectoralis (Ramus superior of Melnikoff). This vein commences within the lung below the subclavian groove, in the apicopectoral plane. Following this plane downwards and backwards it passes to the lateral side of the apical bronchus to end by uniting with the apicoposterior vein on the lateral side of the end of the upper lobe bronchus. It receives tributaries from deeper parts and the costal surface of the adjacent segments. Tributaries at its upper end commonly communicate in the intersegmental plane with a deep tributary of the anterior descending vein (V. apicopectoralis medialis).

V. apicoposterior (V. apicalis of Herrnheiser & Kubat) commences near the posterior surface below and behind the apex of the lung, in the apicoposterior plane, i.e. between the posterior apical bronchus and the superior branch of the posterior terminal bronchus. It drains the deeper parts and costal surfaces of these segments, commonly also the mediastinal surfaces. Its largest branch is usually a posterior terminal vein (V. axillaris posterior of Herrnheiser & Kubat) which emerges from within the posterior terminal subsegment (figured but not labelled in Figs. 16, 21) and often receives veins from the interlobar surface. The apicoposterior vein ends by joining the apicopectoral vein as stated above.

V. magna lobi superioris—the great upper lobe vein (Figs. 3, 16, 21 and 26) (Ramus posterior of Herrnheiser & Kubat). This vein is in most lungs

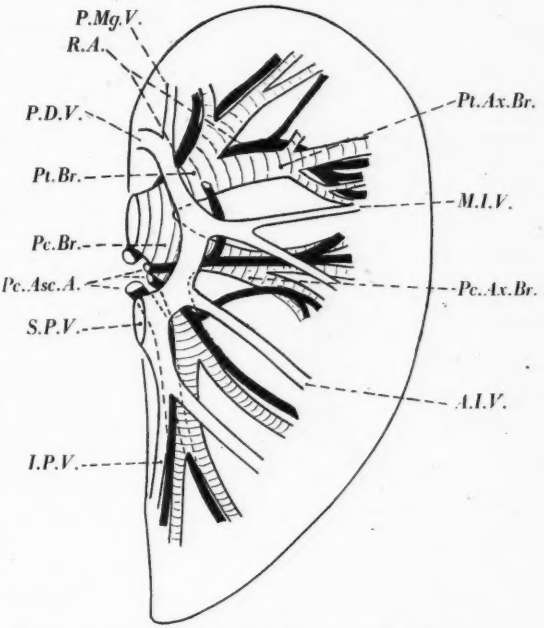


Fig. 17. Interlobar surface of right upper lobe, dissected (venous type, p. 119); bronchi with cross lines, arteries in black, veins white. Lettering of bronchi and arteries as in Figs. 14, 15, of veins as in Fig. 16. *P.Mg.V.* posterior marginal vein.

the principal vein of the upper lobe. It commences on the lateral side of the end of the upper lobe bronchus or the base of one of the bronchi that arise from it. It is formed by the union of the apicopectoral and apicoposterior veins. It passes obliquely forwards and medially beneath the lateral end of the upper lobe bronchus and the pectoral artery (from which it is separated by lymph glands) to join the posterolateral aspect of the superior pulmonary vein (Figs. 3, 5). It is separated by lymph glands from the angle of junction of the two divisions of the pulmonary artery. Anteriorly it is

concealed by the anterior descending vein at the line of reflexion of the pleura, and by the overlapping margin of the lung. The pectoral ascending artery arches over above it in the majority of lungs. Posteriorly it is concealed by lymph glands and by the origin of the posterior ascending artery. It is adjacent to the pleura within the posterior part of the horizontal fissure, and forms a conspicuous feature on interlobar approach to the hilum (Figs. 11, 18). Its tributaries, other than the two which unite to form it, are as follows: anterior interlobar, posterior interlobar, posterior marginal and posterior descending (see superficial veins).

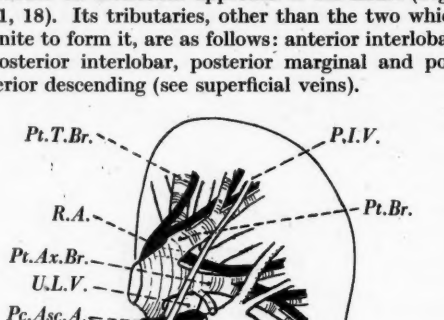


Fig. 18. Interlobar surface of right upper lobe, dissected (intermediate between arterial and venous types, pp. 118, 119); extensive distribution of the recurrent artery; posterior segment drained mainly by deep veins. Lettering as in Figs. 14, 15 (arteries and bronchi), and Fig. 16 (veins). *P.I.V.* posterior interlobar vein.

Superficial veins

Mediastinal surface (Figs. 16, 21). There are two veins in the anterior portion of the surface, the anterior descending and the inferior pectoral, and one vein in its posterior portion, the posterior descending vein.

(1) V. descendens anterior (V. subpleuro-mediastinalis of Herrnheiser & Kubat) has a nearly vertical subpleural course immediately anterior to the root of the lung. It varies greatly in size. Its junction with the superior pulmonary vein is anterior to the pulmonary artery (truncus inferior) in the root of the lung (Figs. 1–3). At a higher level this vein is medial to the pectoral bronchus and artery. It generally receives two superficial tributaries which drain the medial surfaces of the pectoral segment (V. sterno-medialis of Herrnheiser & Kubat) and of the apical segment, but either of them may be absent. It also commonly receives two deep veins, (1) V. apicopectoralis medialis, mentioned above, from the apicopectoral plane, and (2) V. apicalis which emerges from between the anterior and posterior apical subsegments and passes forwards either medially (Fig. 16) or laterally to the anterior apical bronchus.

(2) V. pectoralis inferior (the pectoral mid-sternal vein of Ewart) runs horizontally close to the mediastinal pleura below the level of the pectoral artery and bronchus. It joins the superior pulmonary vein at the reflexion of pleura from the lung on to this vein (Figs. 2, 3 and 16).

It may be large, draining the greater part of the pectoral segment, or it may be small and drain only a small part where the mediastinal and interlobar surfaces meet.

(3) V. descendens posterior (the posterior ascending vein of Ewart) is occasionally large (Fig. 25) but is more often inconspicuous or absent (Figs. 5, 21A, 23). It proceeds downwards beneath the pleura of the lung behind the root and joins the great upper lobe vein. It thus passes medially to the posterior bronchus and posterior ascending artery. When the latter contributes a branch to the lower lobe (dorsal segment), this branch hooks over the lower end of the vein (Figs. 5, 25). This vein provides a route that is alternative to the anterior descending vein for blood from the mediastinal region of the apical segment. When it is absent the blood of the posterior mediastinal region is drained by perforating veins which dive into the lung to join deep tributaries of the apicoposterior vein. It sometimes is joined by a large vein from the dorsal segment of the lower lobe (cf. Fig. 11); the oblique fissure is then incomplete posteromedially. Alternatively it may (Fig. 20) end as a descending communicating vein which goes into the lower lobe and thus drains eventually into the inferior pulmonary vein. This occasional arrangement gives rise to the appearance which is sometimes interpreted as an abnormal superior pulmonary vein (p. 111).

Interlobar surface (Figs. 17, 18, 19, 23 and 24). Superficial veins are commonly arranged so as to alternate with and lie in the interspaces between the larger bronchi of this region (Fig. 17); the posterior part of the surface is sometimes devoid of large superficial veins, and the blood then passes by perforating veins into deep veins (Fig. 18). *Anterior, middle* and *posterior interlobar veins* are distinguished, and a *posterior marginal vein* (Fig. 16).

(1) *V. interlobaris anterior* (V. obliquus inferior of Melnikoff; V. pectoralis of Herrnheiser & Kubat). This vein drains the anterior part of the interlobar

surface. It may be represented by two veins which open separately into the superior pulmonary vein. Close to its termination there is a considerable mass of (subpectoral) lymph glands on its medial side in the hilum of the lung; this vein is, however, readily seen on interlobar approach through the horizontal fissure. It may drain sometimes into the middle interlobar or inferior pectoral vein (Fig. 7).

(2) *V. interlobaris media* (V. axillaris partim of Herrnheiser & Kubat). This vein drains the region of junction of the pectoral and posterior segments, and is thus opposite the junction of the horizontal and oblique fissures of the lung. It joins the great upper lobe vein by passing below the lateral end of the upper lobe bronchus, close to the interlobar pleura (Figs. 17, 19, 22).

(3) *V. interlobaris posterior*, often absent, drains the lower part of the posterior segment. It joins the great lateral vein close to the interlobar pleura, sometimes in common with posterior marginal or a posterior descending vein (Figs. 18, 26).

Variations in venous drainage (Figs. 16, 21)

These consist largely in differences in relative size of veins described above. The usual pattern (type 1) is shown in Fig. 16. In type 2 (Fig. 21 A) the anterior descending vein is very large and extends its drainage area by receiving blood from the apicoposterior plane as well as from the apicopectoral plane. The great upper lobe vein is then reduced to a small collecting channel from the superficial interlobar veins.

Two or three variants combine in type 3 (Figs. 11, 21 B) to produce a large drainage area for the great upper lobe vein in combination with a very small anterior descending vein, brought about by (1) encroachment by a large posterior descending vein on the superficial medial drainage area below the apex, (2) drainage from the apicopectoral plane solely by the apicopectoral vein into the great upper lobe vein, and (3) drainage of the dorsal segment of the lower lobe into the great upper lobe vein by an ascending communicating vein. A fourth venous pattern is provided by type 4 (Fig. 20) in which drainage of the apicoposterior vein, including the whole of the posterior segment, is effected by a descending communicating vein that carries blood through the dorsal segment of the lower lobe to the inferior pulmonary vein.

Minor variations in the veins of the interlobar surface have been described above. Anterior interlobar veins vary in their manner of connexion with the superior pulmonary vein. The posterior parts of the interlobar and mediastinal surfaces may drain like the costal surface by *perforating* veins that dive into the lung to join the deep veins of segmental planes (Fig. 18).

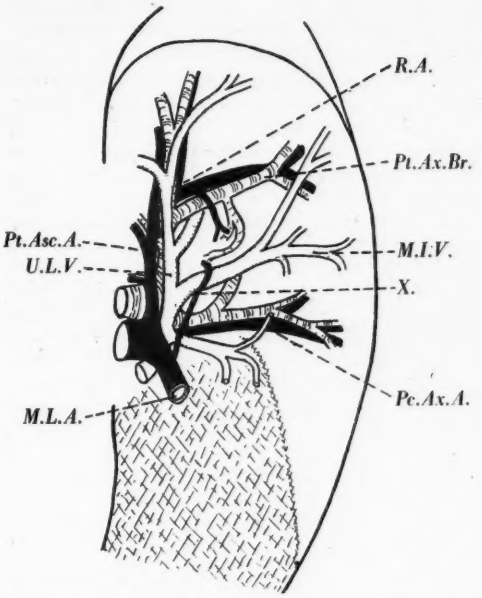


Fig. 19. Interlobar surface of right upper lobe after removal of coalesced middle lobe (arterial type, p. 118); the middle lobe artery provides an ascending artery, *X*, to a small part of the posterior axillary subsegment (cf. Fig. 9K). Lettering as in Figs. 14, 15 (arteries and bronchi) and Fig. 16 (veins). *M.L.A.* middle lobe artery.

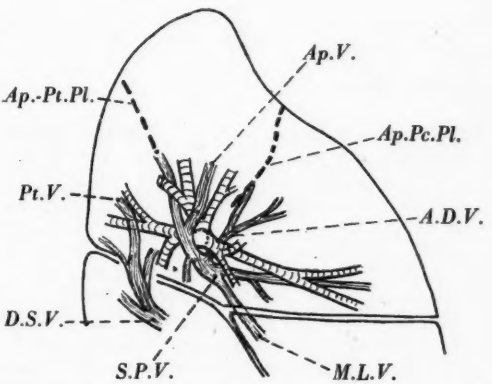


Fig. 20. Venous drainage of upper lobe (lateral, i.e. costal view), veins shaded, bronchi with cross lines, showing large communicating veins. Lettering as in Fig. 16. *D.S.V.* vein of dorsal segment of lower lobe draining blood from posterior segment of upper lobe; *M.L.V.* middle lobe vein; *S.P.V.* termination of superior pulmonary vein.

Approaches to the bronchovascular pedicle of the upper lobe

Anterior approach (Figs. 1, 3). In the small portion of the root between the pericardium and pleural reflexion on to the lung there is seen above, a small triangular part of the right bronchus, below this the truncus superior (upper division) of the pulmonary artery. Next below is a triangular interval which contains lymph glands between the truncus superior and truncus inferior of this artery. At a lower level the truncus inferior is not readily distinguishable from the superior margin of the superior pulmonary vein, which (with its anterior descending tributary) partly covers it; a fascial extension from the pericardium unites the vein to the sheath of the artery.

In the part of the hilum exposed by turning back the lung margin, the branches of the truncus runs directly backwards above the upper lobe bronchus next the mediastinal pleura above the root. Variations which affect the identification of the arteries have been described on p. 105.

Below the point of entry of the anterior descending vein into the superior pulmonary vein are seen the terminations of the inferior pectoral and anterior interlobar veins, and, lower still, of veins from the middle lobe draining into the superior pulmonary vein (Fig. 3).

On deeper dissection of the hilum, after ligature of the anterior descending and inferior pectoral veins, the interval between the superior pulmonary vein and the pectoral artery is exposed. Its lateral part is occupied by a parabronchial portion of the pectoral segment of the lung, its medial part by lymph glands. If the glands are pulled away from the lung the great upper lobe vein is exposed, joining

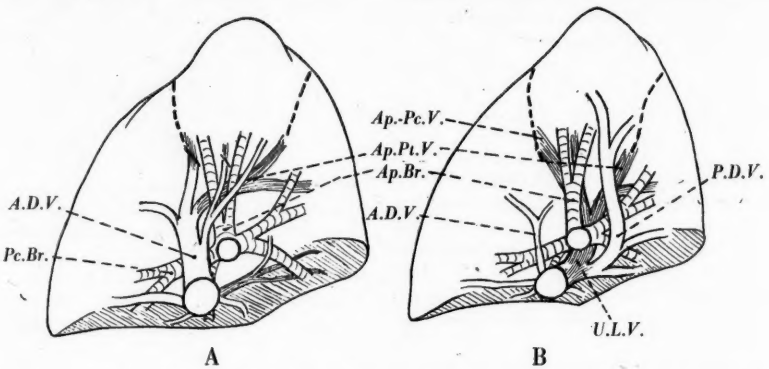


Fig. 21. Venous drainage of upper lobe (medial view), showing two main types of variation. In A (type 2) there is a large anterior descending vein which collects most of the blood from the interior as well as from the surfaces of the upper lobe; in B (type 3) there is a small anterior descending vein and large posterior descending vein: the great upper lobe vein thus collects most of the blood from the apical and posterior segments. Lettering as in Fig. 16.

superior of the pulmonary artery occupy the highest position (Figs. 1, 3, 7). There may be two, three or four separate branches visible (p. 105). The anterior descending vein, usually a large vessel, is seen to cross the lowest of these arteries, the pectoral; if this vein is followed upwards it is found to enter the plane between pectoral and apical segments in the direction of the subclavian groove, besides receiving superficial tributaries from the mediastinal surface. Above the pectoral artery the apical artery, a branch of the truncus superior, is seen to incline upwards and laterally into the lung. When a third artery is visible above the other two this is generally the posterior apical artery (p. 105), which often (within the lung) gives origin to a recurrent artery for the posterior lobe.

The recurrent artery, when arising low down (Figs. 5, 7, 8) is not easily seen from in front and is easily overlooked in an anterior approach, since it the deep aspect of the superior pulmonary vein. A small pectoral ascending artery commonly arches over it to reach the lower part of the pectoral segment (Fig. 3). Exceptionally (Fig. 8), this artery may be of large size and partially or completely replace the pectoral artery (ordinarily a branch of the truncus superior).

Posterior approach (Fig. 5). The posterior aspect of the right bronchus is seen on removal of the pleura of the root. A bronchial artery usually runs down its posterior aspect and gives off a branch that turns over the upper aspect of the bronchus.

When the pleura is incised and the lung margin turned laterally, a large posterior descending vein may be encountered just behind the root structures (Figs. 5, 23) and a branch of the posterior ascending artery to the lower lobe may be seen hooking over it. The junction of the upper lobe bronchus with the main bronchus is seen just above a mass of lymph

glands. These conceal the pulmonary artery (lower division) and origins of the posterior ascending and dorsal segment arteries. Further inside the lung the posterior and apical bronchi join just above the great upper lobe vein (the latter accessible with difficulty on account of the posterior descending vein and posterior ascending artery). The posterior ascending artery, very variable in size, generally proceeds towards the posterior bronchus and supplies a variable portion of the posterior segment. It may be represented by two branches with or without a short common stem. Above the upper lobe bronchus there is seen the apical, or the posterior apical artery, which passes upwards and laterally into the lung on the medial side of the apical bronchus, and there is, in addition, in some lungs, a recurrent artery that arches over the upper lobe bronchus and proceeds towards the deep aspect of the posterior bronchus (Fig. 5).

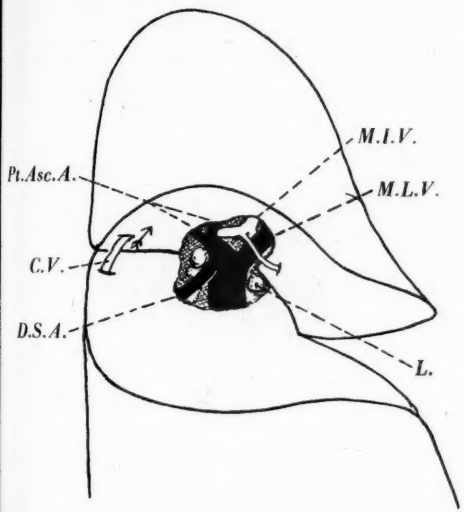


Fig. 22. Interlobar approach to hilum of a right lung through the oblique fissure, arterial type (cf. Figs. 4, 23). The inferior division of the pulmonary artery is exposed where it gives off arteries to the upper, middle and lower lobes. No large vein conceals the posterior ascending artery to the upper lobe. *L.* lymph glands; *M.I.V.* middle interlobar vein. Other lettering as in Fig. 4.

Interlobar approach (Figs. 4, 10, 11, 12 and 22). This approach is in many lungs only to be made through the posterior part of the oblique fissure on account of the incompleteness of the horizontal fissure; the part that is incomplete is crossed by small veins. The medial part of the upper lobe is also sometimes fused to the lower lobe of the lung behind the bronchovascular pedicle. A large vein is commonly present in this zone of union; it either drains blood from the posterior segment into the lower lobe and so to the inferior pulmonary vein, or it drains blood from the lower lobe into the upper lobe veins (Figs. 11, 20).

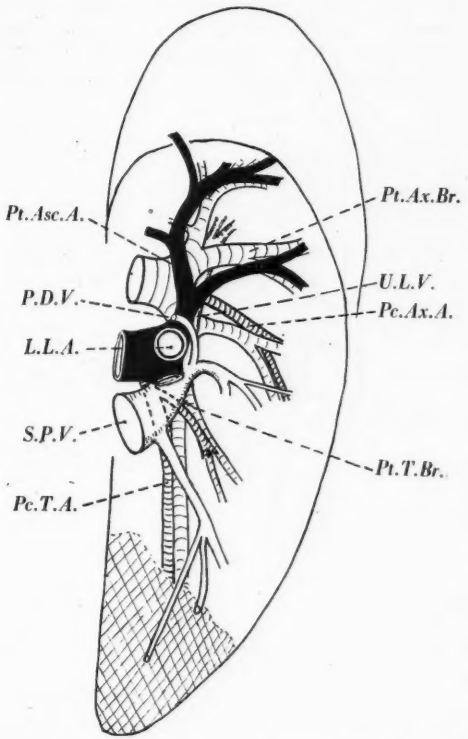


Fig. 23. Interlobar surface of right upper lobe dissected (arterial type). A large posterior ascending artery supplies the whole of the posterior segment; it is separated from the interlobar pleura only by a very small posterior descending vein (cut short in figure). Veins draining a part of the middle lobe join the upper lobe veins where the two lobes are coalesced over a small area. Arteries from lower division of pulmonary artery in black, those from upper division with heavy cross lines; bronchi with thin cross lines. *L.L.A.* lower lobe artery; *S.P.V.* superior pulmonary vein. Other lettering as in Figs. 14, 15 (arteries and bronchi), and Fig. 16 (veins).

Approach through the *oblique* fissure. In many lungs no other interlobar approach is possible on account of the absence of a horizontal fissure. On division of the pleura in the depth of the oblique fissure, the vascular pattern differs according to the relative size and course of arteries and veins. We may distinguish a venous and an arterial type ac-

cording to which are the more conspicuous vessels; the latter is the more common.

The differences depend primarily on (1) the venous pattern of the posterior segment of the upper lobe, and (2) the size of the posterior ascending artery.

Type 1. *Arterial type* (Figs. 4, 19, 22 and 23). Diverging branches of the inferior division of the pulmonary artery are seen, viz. a conspicuous posterior ascending artery passing upwards, one or two middle lobe arteries passing forwards, the lower lobe

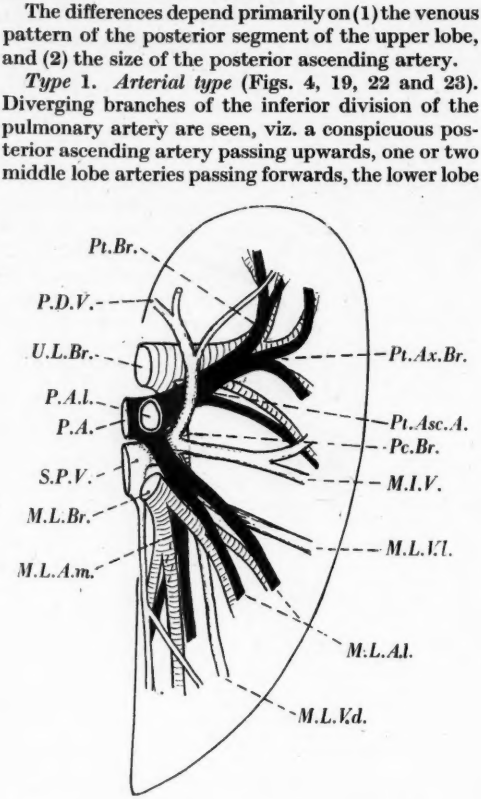


Fig. 24. Interlobar surface of right lung with coalesced upper and middle lobes (intermediate type of interlobar approach, interlobar veins and ascending arteries to posterior segment large and of similar size. *M.L.A.l.* lateral branches of middle lobe artery; *M.L.A.m.* medial branches of middle lobe artery; *M.L.Br.* middle lobe bronchus; *M.L.V.l.* lateral middle lobe vein; *M.L.V.d.* deep middle lobe vein; *P.A.* right pulmonary artery; *P.A.l.* lower lobe artery; *S.P.V.* superior pulmonary vein; *U.L.Br.* upper lobe bronchus. Other lettering as in Figs. 15 and 16.

artery downwards and backwards, and just within the lower lobe, the dorsal segment artery of the lower lobe. The posterior ascending artery proceeds upwards into the posterior segment of the upper lobe; it may divide into two, almost at once. It may give a branch to the pectoral axillary subsegment just above the horizontal fissure (i.e. a common origin for pectoral and posterior ascending arteries). It may share an origin with the dorsal segment artery of the lower lobe.

Lymph glands are seen (1) posteriorly to the origin of the posterior ascending artery, (2) laterally to the inferior division of the pulmonary artery, and (3) anteriorly, in the angle between middle and lower lobe arteries. In this (arterial) type only small veins are readily accessible close to the pleura of the fissure, the drainage of the adjacent parts of the lung being effected through the alternative pathways, e.g. through the deep vein of the posterior segment. A middle lobe vein may cross the origin of one or both of the two middle lobe arteries, to enter the hilum anteriorly to the posterior ascending artery (Fig. 22). Small posterior descending and posterior

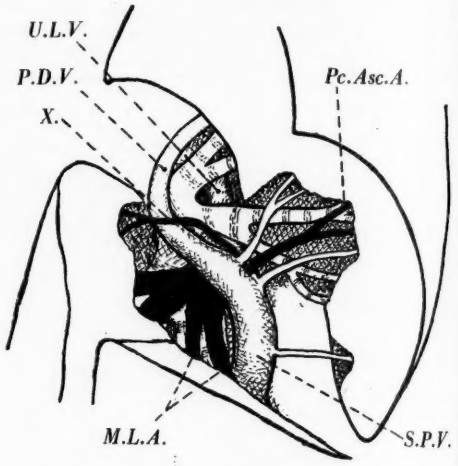


Fig. 25. Interlobar approach through oblique and horizontal fissures (venous type), cf. Fig. 23. A large posterior descending vein joins the great upper lobe vein close to the base of the pectoral bronchus. It is crossed by a small branch of the pectoral ascending artery to the lower lobe; there is no posterior ascending artery. *M.L.A.* middle lobe arteries; *U.L.V.* great upper lobe vein; *X*, branch of pectoral ascending artery to lower lobe. Other lettering as in Figs. 14, 15 and 16.

interlobar veins may be present and cross the posterior ascending artery to enter the hilum anteriorly to this artery. These may, however, be absent or join deep veins in the posterior lobe without presenting themselves in this exposure. If these veins are large the vascular pattern becomes that of the venous type.

On deeper dissection, the angle of junction of middle and lower lobe bronchi is found in the angle between corresponding arteries, covered by the above-mentioned lymph glands. The upper lobe bronchus is deep to the posterior ascending artery; its subdivision can be seen when the artery is absent. The great upper lobe vein is deeply situated

in the angle between posterior ascending and middle lobe arteries (Fig. 4).

Type 2. *Venous type* (Figs. 10, 11, 17, 18). A large vein skirts the hilum above an exposed portion of the pulmonary artery (lower division). It crosses the posterior ascending artery, almost concealing it from view. A small branch of the posterior ascending artery may, however, hook over the vein to reach the lower lobe (dorsal segment). The origins of the middle lobe and dorsal segment arteries can be found just below the large vein. This vein is formed by the union of one or more of the following: posterior descending, posterior marginal,

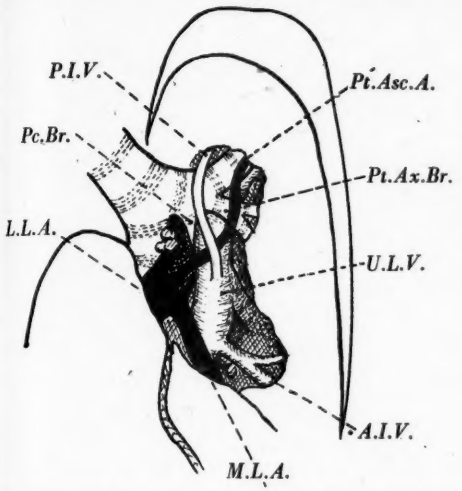


Fig. 26. Interlobar approach through oblique and horizontal fissures (intermediate type). A considerable length of the great upper lobe vein is exposed. A small artery and vein partially obscure the posterior bronchus. *A.I.V.* anterior interlobar veins; *L.L.A.* lower lobe artery; *M.L.A.* middle lobe artery; *Pc.Br.* base of pectoral bronchus; *Pt.Ax.Br.* posterior axillary bronchus; *P.I.V.* posterior interlobar vein; *Pt.Asc.A.* posterior ascending artery; *U.L.V.* upper lobe vein.

posterior interlobar, from the upper lobe, or a communicating vein passing between upper and middle lobes. The difference of appearance between extreme examples of the arterial and venous types is due primarily to the relative size of this vein and of the posterior ascending artery.

Approach through the oblique and horizontal fissures. When an approach to the hilum is made through both the fissures which are below the upper lobe instead of through the oblique fissure alone, the middle lobe vessels are differently orientated and the greater upper lobe vein is more accessible (Figs. 25, 26). A considerable length of this vein is seen above the middle lobe arteries and in front of the posterior ascending artery. The vein finally disappears from view posteriorly under cover of the origin of the posterior bronchus from the upper lobe bronchus. In the posterior part of the field the vascular pattern falls into the venous or arterial type as described for the approach through oblique fissure alone.

The two vascular patterns described above as arterial and venous types are not so common as an intermediate pattern which is illustrated in Figs. 24 and 26. Neither the arteries nor the veins are so large as to be the predominant feature.

Relative sizes of posterior ascending and recurrent arteries. The size of the posterior ascending artery or arteries is, almost invariably, inversely proportional to that of the recurrent artery, since these two arteries, between them, generally supply the whole of the posterior segment. Since the recurrent artery may be somewhat inaccessible at the hilum of the lung in the living subject, while the posterior ascending artery can be easily examined through the oblique fissure, this interlobar approach affords a convenient means of a preliminary assessment of the arterial supply of the posterior segment. Only in exceptional instances will a small posterior ascending artery coexist in the same lung with a small recurrent artery, viz. in those lungs in which the pectoral axillary artery contributes largely to the supply of the posterior segment (Figs. 14A, 15B).

SUMMARY

1. The arterial and venous pattern of the right upper lobe has been examined in a series of fifty lungs with special reference to the distribution of the larger branches seen at the hilum in the bronchopulmonary segments.

2. The upper division or truncus superior of the right pulmonary artery generally divides into two or three branches, viz. the pectoral, apical and recurrent (the last-named being absent nearly as often as it is present). Unusual arterial patterns are also described.

3. The pectoral artery is generally the main artery of supply to the pectoral segment; it is crossed superficially near its origin by the anterior descending vein.

4. The apical artery is the main artery of the apical segment.

5. The recurrent artery turns sharply backwards above the upper lobe bronchus and supplies some part of the posterior segment. The size of this artery is generally inversely proportional to that of the posterior ascending artery (from the lower division or truncus inferior of the pulmonary artery) the size of which can be readily ascertained by an interlobar approach through the oblique fissure.

6. The lower division (truncus inferior) of the pulmonary artery almost always contributes one or

more arteries, named ascending arteries, to the supply of that part of the upper lobe which is not supplied from the upper division (truncus superior). These arteries are distributed primarily with the bronchi adjacent to the interlobar surface; but sometimes they have a wider distribution in the pectoral or posterior segments so as to form their main or sole supply (a feature which is of considerable frequency in the posterior segment but is unusual in the pectoral segment). Ascending arteries to the pectoral segment are generally inaccessible by an interlobar approach on account of the more laterally placed great vein of the upper lobe. Ascending arteries to the posterior segment are, on the other hand, readily accessible by an approach through the posterior part of the oblique fissure.

7. Superficial veins run close to the interlobar and mediastinal surfaces. They are less constantly present in the posterior than in the anterior parts of these surfaces.

8. Large deep veins characteristically lie in the planes between segments and subsegments and have been named accordingly. They drain mainly into a great upper lobe vein that passes below the base of the pectoral bronchus to join the deep (lateral) aspect of the superior pulmonary vein. These deep veins drain the region of the costal surface and commonly also the posterior parts of the interlobar and mediastinal surfaces.

9. Veins sometimes pass between the upper lobe and the other lobes when the oblique or horizontal fissures are incomplete; they may be large and convey blood from the upper lobe to the inferior pulmonary vein behind the right bronchus, or alternatively, from the lower or middle lobes into the venous system of the upper lobe.

The various appearances presented on anterior, posterior and interlobar approach to the hilum are described.

10. The great variety of appearances presented, when an interlobar approach is employed, is due to vascular variations in the posterior segment of the upper lobe; two extreme types of appearance are recognized, the arterial and the venous.

11. Examination of the posterior ascending artery through the oblique fissure affords the readiest means of a preliminary assessment of the source of the arterial supply of the posterior segment.

REFERENCES

ADACHI, B. (1933). *Das Venensystem der Japaner.* Kyoto.

AEBY, C. (1880). *Der Bronchialbaum der Säugethiere und des Menschen.* Leipzig.

APPLETON, A. B. (1944). *Lancet,* 4 Nov., p. 592.

BACKMANN, G. (1924). *Läk för. Förh.* **29**, 345.

BARRETT, N. R. (1938). *St Thomas's Hosp. Rep.* 2nd Ser. **3**, 139.

BATTS, M. (1939). *J. Thorac. Surg.* **8**, 565.

BROCK, R. C. (1942). *Guy's Hosp. Rep.* **91**, 111.

CLELAND, W. P. (1941). *Brit. J. Tuberc.* **35**.

EAST, T. & BARNARD, W. G. (1938). *Lancet,* Vol. 1, p. 834.

EWART, W. (1888). *The Bronchi and Pulmonary Blood Vessels.* London.

FAGAN, P. J. (1893). *Trans. R. Acad. Med. Ire.* **11**, 508.

FELIX, R. (1930). *Chirurgie der Brustorgane.* Berlin.

FOSTER CARTER, A. F. (1942). *Brit. J. Tuberc.* **36**, 19.

GLASS, A. (1934). *Amer. J. Roentg.* **31**, 328.

HASSE, C. (1892). *Arch. Anat. Phys.* (Anat. Abt.), **5–6**, 324.

HERRNHEISER, G. & KUBAT, A. (1936). *Z. ges. Anat.* 1. *Z. Anat. EntwGesch.* **105**, 570.

HOVELACQUE, P., MONOD, O. & EVRARD, H. (1937). *Le Thorax.* Paris.

HYRTL, J. (1837). *Med. Jb. Oesterr,* **18**, 3.

INGALLS, N. W. (1932). *Anat. Rec.* **53**, 269.

KENT, E. M. & BLADES, B. (1942). *J. Thorac. Surg.* **12**, 18.

KRAMER, R. & GLASS, A. (1932). *Ann. Otol., etc., St Louis,* **41**, 1210.

LUCIEN, M. & WEBER, P. (1936). *Arch. Anat., Strasbourg,* **21**, 109.

MACCREADY, P. B. (1918). *Bull. Johns Hopk. Hosp.* 29, 271.

MELNIKOFF, A. (1924). *Z. ges. Anat.* 1. *Z. Anat. EntwGesch.* **71**, 186.

MENKE, J. F. (1936). *Anat. Rec.* **65**, 55.

MILLER, W. S. (1937). *The Lung.* Baltimore.

NARATH, A. (1901). *Der Bronchialbaum der Säugetiere und des Menschen, Bibliotheca med.,* Abt. A. Stuttgart.

NEIL, J. H., GILMOUR, W. & GWYNNE, F. J. (1937). *Med. J. Aust.* **2**, 109.

NELSON, H. P. (1932). *J. Anat., Lond.,* **66**, 228.

PEIRCE, C. B. & STOCKING, B. W. (1939). *Ann. Rev. tuberc.* **39**, 516.

TESTUT, L. (1930). *Traité d'Anat.* (*Latarjet*), p. 957. Paris.

THE ECHIDNA-PTERYGOID

By H. LEIGHTON KESTEVEN, *Australian Museum, Sydney*

Parrington & Westoll (1940) have advanced evidence which leads them to believe that the ectopterygoid of the saurian palate is represented in the therian palate by the echidna-pterygoid of the monotremata and by the ventral moiety of the pterygoid of the ditremata.

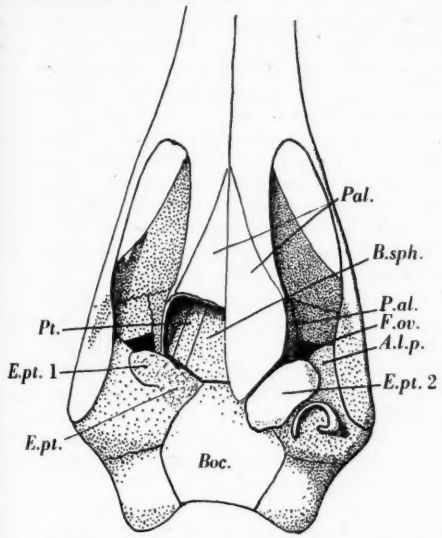


Fig. 1. Palatal view of the skull of *Echidna*. *A.l.p.* alisphenoid lamina of the periotic bone; *Boc.* basioccipital bone; *B.sph.* basisphenoid bone; *E.pt.* echidna-pterygoid; *E.pt.* 1, *E.pt.* 2 echidna-pterygoid with the outer table of the bone and the tympanic component removed (1, the portion of the bone which contributes to the cranial floor; 2, the portion fastened to the venter of the periotic, and suturing with the basisphenoid, basioccipital, pterygoid and palatine bones); *F.ov.* foramen ovale; *Pal.* palatine bone, cut away on the right side of the skull to show the position of the pterygoid; *P.al.* processus alaris; *Pt.* pterygoid bone.

Watson (1916) and Kesteven (1918) had proposed to recognize the echidna-pterygoid as the homologue of the tympanic wing of the alisphenoid. This view was opposed by de Beer & Fell (1936), who believed that they had found, in *Ornithorhynchus*, a separate alisphenoid bone ossifying in the lateral part of the basisphenoid cartilage. Kesteven (1940) demonstrated that the alisphenoid bones of de Beer & Fell were not separate ossifications, but only two of the three centres of ossification of the basisphenoid, confirming an earlier statement to that effect by Kesteven & Furst (1929).

It is questionable whether any phylogenetic significance attaches to the occasional development of the therian pterygoid from two ossific centres, but, if such dual ossification has significance, then Parrington & Westoll are probably correct in homologizing the therian ventral moiety with the saurian ectopterygoid.

Parrington & Westoll were unaware of the work of Kesteven & Furst (1929) and of Kesteven (1940), and accepted the statement of de Beer & Fell (1936) that a separate alisphenoid bone is present in the monotreme skull.

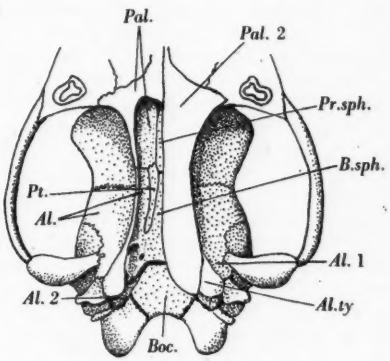


Fig. 2. Palatal view of the skull of *Thylacinus*. *Al.* alisphenoid bone; *Al.*1 the portion which corresponds to *E.pt.* 1 in *Echidna*; *Al.*2 the portion which corresponds to *E.pt.* 2 in *Echidna*; *Pr.sph.* presphenoid; other lettering as in Fig. 1.

Whilst it must be admitted that the series of fossil palates illustrated and described by them strongly supports the view they take, it is probable that Parrington & Westoll give undue weight to the palatal topography of the echidna-pterygoid, and too little to other features, possibly influenced by the belief that another alisphenoid bone is present in the skull.

Presumably none will deny that the echidna-pterygoid is identical in both monotremes: it remains to decide whether that of *Echidna* has acquired parts not present in that of *Ornithorhynchus*, or whether the latter has lost parts present in the former.

If the monotreme echidna-pterygoid is regarded as a modified form of the ectopterygoid of the cynodonts, it is extremely difficult to imagine how it came to acquire relations and functions in connexion with the formation of the walls of both the cranial

cavity and the auditory organ, for it is completely removed from these in reptiles. Again, if its form in *Ornithorhynchus* were the primitive, it is still difficult to understand why, in *Echidna*, it should have expanded to share in the formation of a cranium already completed by other bones. There is no evidence of any tendency towards the production, in the cranial wall, of a deficiency incapable of being made good by direct extension of adjacent cranial bones: whilst, on the other hand, it is easily credible that the small contribution to the cranial wall made by the bone in *Echidna* could have been provided by extension of the surrounding cranio-mural elements.

It may safely be assumed, therefore, that the form of the bone in *Echidna* is the more primitive of the two.

It has already been stressed that it is extremely difficult to imagine the cynodont ectopterygoid acquiring the otic and cranio-mural parts of the echidna-pterygoid. On the other hand, consideration of the close morphological resemblance between the echidna-pterygoid and the tympanic wing of the marsupial alisphenoid renders more acceptable the concept of the echidna-pterygoid as a reduced alisphenoid rather than an enlarged ectopterygoid. The resemblance is striking in various marsupial species, more particularly in *Thylacinus*, to which attention was drawn recently (Kesteven, 1941).

There is little doubt that the palatine bones in the monotremes present a condition peculiar to the group, and that their extraordinary posterior extension is without significance in relation to the evolution of the mammalian palate. Relations which the palatine bone in these animals bears to the echidna-pterygoid are due to this peculiar backward extension of the former bone, and, therefore, should not be given undue weight as evidence relative to the homology of the latter.

In the illustration of the *Echidna* skull (Fig. 1) the palatine bone on the right side has been cut back to something approaching the normal size of the bone in the tetrapods generally. The outer table of the echidna-pterygoid together with the contribution of the bone to the tympanic bulla has been removed. This procedure displays the ascending lamina of the palatine, the posterior portion of the pterygoid, and the relations of the echidna-pterygoid to the basisphenoid, basioccipital, pterygoid, palatine and petrosal bones.

In the illustration of the skull of *Thylacinus* (Fig. 2) the corresponding relations of the tympanic wing of the alisphenoid bone can be seen on the right side of the skull. On the left side the palatine has been fancifully extended posteriorly to meet that portion of the alisphenoid which contributes to the formation of the tympanic bulla. It will be obvious that this fanciful extension has brought about, between the tympanic wing of the alisphenoid and all the other bones, relations which reproduce essentially those of the echidna-pterygoid to the corresponding cranial elements in *Echidna*.

The weight of evidence therefore favours the conclusion that the echidna-pterygoid is a much-reduced alisphenoid bone.

REFERENCES

DE BEER, G. R. & FELL, W. A. (1936). *Trans. Zool. Soc. Lond.* **23**.

KESTEVEN, H. L. (1918). *J. Anat., Lond.*, **52**, 449.

KESTEVEN, H. L. (1940). *Proc. Linn. Soc. N.S. Wales*, **65**.

KESTEVEN, H. L. (1941). *Proc. Linn. Soc. N.S. Wales*, **66**.

KESTEVEN, H. L. & FURST, H. C. (1929). *J. Anat., Lond.*, **63**, 447.

PARRINGTON, F. R. & WESTOLL, T. S. (1940). *Philos. Trans.* B, **230**, 305.

WATSON, D. M. S. (1916). *Philos. Trans.* B, **207**.

NOTE ON THE PALAEONTOLOGY OF THE LEMUROID BRAIN

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Whilst the lemurs are now generally accepted as true Primates (though allocated to a separate sub-order, the Lemuroidea), they show many aberrant features in their anatomy which contrast rather sharply with the organization of the higher Primates. Among these divergent characters is the convolutional pattern of the cerebral cortex. This formed the subject of an extensive monograph by Elliot Smith in 1902*a*, in which he concluded that, despite certain differences, the lemuroid pattern shows undeniable affinities with that of the Anthropoidea, particularly in the disposition of the calcarine sulcus. Nevertheless, the lemuroid pattern in general follows the primitive plan of eutherian mammals in that the sulci over the dorso-lateral surface of the cerebral hemispheres are disposed longitudinally. Thus, they cut right across the various cortical areas (which are disposed in a number of transverse bands ranged in series from the frontal to the occipital pole). The development of this pattern can be related to mechanical factors which obtain in the ontogeny of the primitive eutherian brain, as discussed elsewhere (Le Gros Clark, 1945). In the monkey's brain, on the other hand, the sulci on the dorso-lateral aspect of the hemisphere are mainly disposed in a transverse direction, forming limiting sulci which mark the boundary lines between adjacent cortical areas (Brodmann, 1909). That this is not a fundamental difference, however, is suggested by the fact that in certain lemuroids such as *Perodicticus* (Brodmann, 1908; C. & O. Vogt, 1907; Zuckerman & Fulton, 1941) and *Indris* (Brodmann, 1908), a transversely disposed sulcus centralis marking the caudal boundary of the area giganto-pyramidalis is developed in a manner quite similar to that found in the Anthropoidea. The question arises whether the generalized longitudinal pattern which characterizes most lemuroid brains represents a truly primitive feature, or whether it is to be included in those primitive features which Elliot Smith suspected to be secondary retrogressive modifications of a more highly developed type of brain. The following brief notes on the endocranial casts of fossil lemuroids are intended as a contribution to the solution of this question.

The earliest lemuroid (and, indeed, the earliest Primate) of which a complete endocranial cast is available is the Eocene species, *Adapis parisiensis*.* The outstanding characters of the cast can be seen by reference to Fig. 1, which may be compared with the endocranial casts of *Tupaia ferruginea*, *Microcebus* and *Lemur catta* shown in Fig. 2. The whole brain is considerably flattened in a vertical direction, so that the temporal lobes splay out on either side to an unusual degree. It shows extremely primitive features in the projecting, pedunculated olfactory bulbs, the small size of the cerebrum in

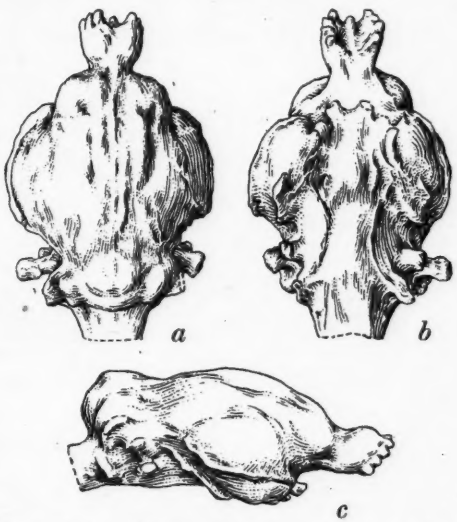

Fig. 1. Endocranial cast of *Adapis parisiensis*: (*a*) dorsal view; (*b*) basal view; (*c*) lateral view. (× 1.)

proportion to the cerebellum, the remarkably slight development of the frontal lobes of the cerebral hemispheres, and the small size of the lateral lobes of the cerebellum. In respect of these features, *Adapis* occupies a position between *Tupaia* and *Microcebus*. On the other hand, the temporal lobe of the *Adapis* brain is proportionately larger than in non-Primate brains of an equivalent size; in this feature the Eocene fossil may be presumed already to show its Primate status, for among the Lemuroidea the relative size of the temporal lobe is a characteristic feature of the brain. The cerebral hemisphere shows two well-marked sulci, a sylvian sulcus extending obliquely upwards and backwards between the frontal and temporal lobes, and a longitudinal sulcus (sulcus lateralis of comparative anatomical nomenclature) extending back from the frontal lobe almost to the occipital region. In this longitudinal folding, the brain of *Adapis* conforms

* A misleading description of a very incomplete endocranial cast of *Adapis parisiensis* has been given by Neumayer (1906).

to the arrangement found in primitive eutherian brains generally.

For comparison with *Adapis*, there are available endocranial casts of four genera of fossil lemurs from Madagascar, which are commonly ascribed to a projecting olfactory peduncles and the forward position of the optic foramina. The fissural pattern, which is clearly marked in the cast, is of the primitive eutherian type, consisting of sulci disposed longitudinally and extending in series over

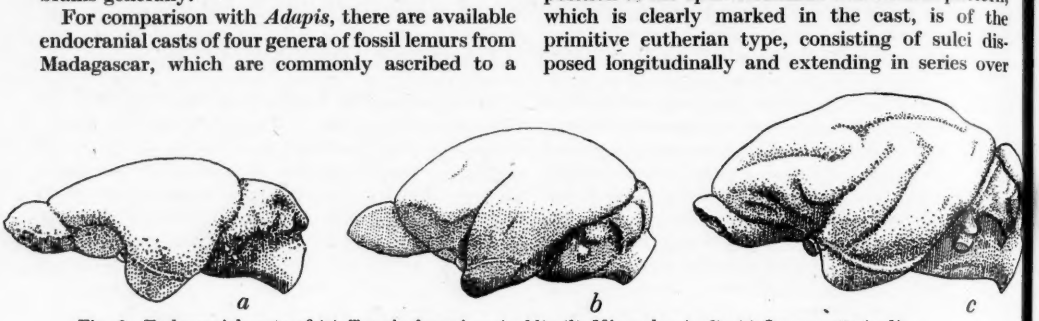

Fig. 2. Endocranial casts of (*a*) *Tupaia ferruginea* (× 1½); (*b*) *Microcebus* (× 2); (*c*) *Lemur catta* (× 1).

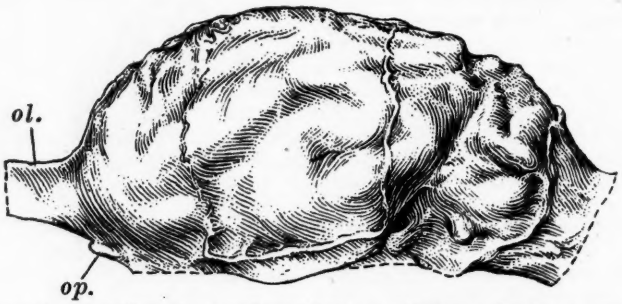

Fig. 3. Endocranial cast of *Megaladapis madagascariensis*: *ol.* olfactory peduncle; *op.* optic nerve (× 1.)

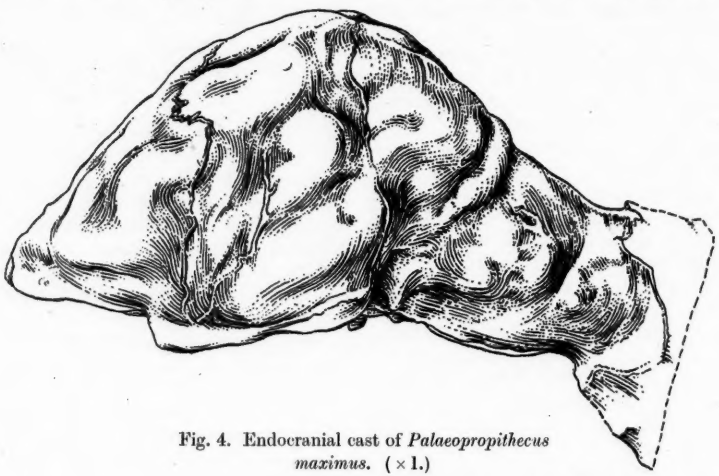

Fig. 4. Endocranial cast of *Palaeopropithecus maximus*. (× 1.)

Pleistocene level. The endocranial cast of *Megaladapis madagascariensis* which was first described by Forsyth Major (1897) and subsequently by Burckhardt (1901) and Elliot Smith (1902 *a*), is shown in Fig. 3. Two outstanding features, which were emphasized by Forsyth Major, are the stout, forward-

the greater part of the length of the hemispheres. A similar pattern also obtains in the endocranial casts of *Palaeopropithecus* (Fig. 4) and *Mesopropithecus* (Fig. 5). Rough diagrams of these interesting specimens have previously been published by Elliot Smith (1908), but it is not altogether easy

to obtain an accurate impression from his sketches of the general convolutional pattern or of the precise position and extent of the individual sulci. In both genera the ventral 'kinking' of the hemisphere has led to the formation of a longer and more pronounced sylvian sulcus, about the posterior extremity of which a well-marked arcuate gyrus has been developed in each case. Thus the general pattern is rather similar to that commonly found in the brains of carnivores.

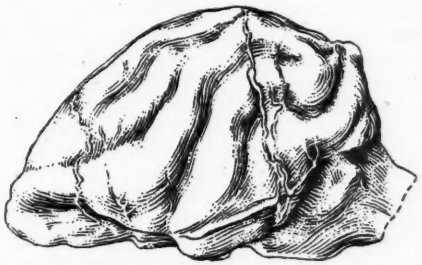

Fig. 5. Endocranial cast of *Mesopropithecus pithecoides*. (×1.)

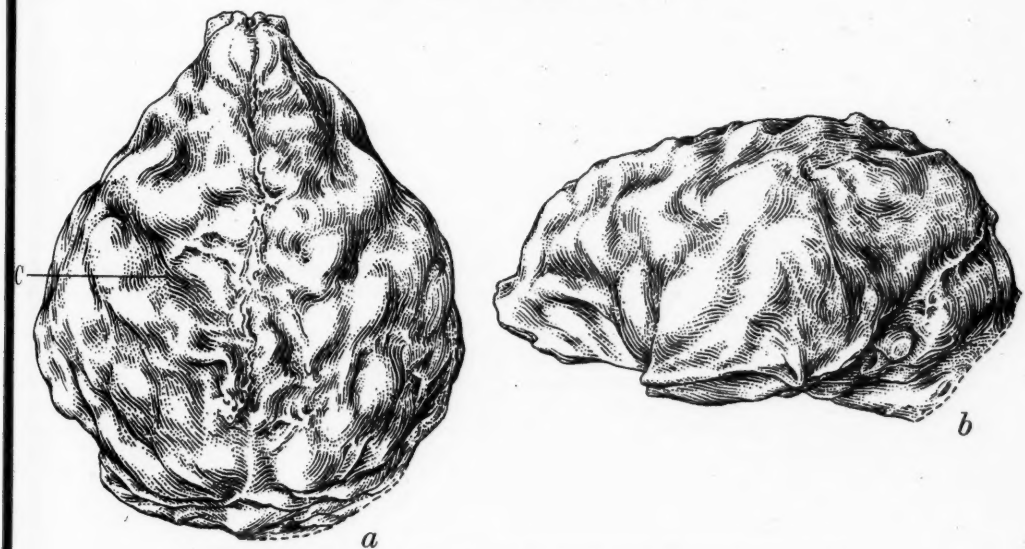

Fig. 6. Endocranial cast of *Archaeolemur*: (*a*) dorsal view; (*b*) lateral view. (×1.)

Of the endocranial casts of fossil lemurs from Madagascar, that of *Archaeolemur* is perhaps the most interesting (Fig. 6). This was originally described by Forsyth Major (1897) and ascribed by him to a new genus (*Globilemur*). Although Grandidier pointed out in 1905 that *Globilemur* was identical with the already recognized genus *Archaeolemur*, the former name has survived for many years and was still employed by Edinger in her outstanding monograph on *Fossil Brains* in 1929. *Archaeolemur* is characterized by a number of remarkably pithecoid features in the skull and dentition, and a consideration of these features was largely responsible for Standing's contention that it is not possible to separate the Lemuroidea and Anthropoidea as separate suborders of the Primates. Elliot Smith remarked on the difficulty of identifying the sulci in the endocranial cast of *Archaeolemur*, and his general conclusions regarding the significance of the sulcal pattern were not very definite. Thus in one publication (1902*a*) he states that the general appearance is 'distinctly pithecoid', in another (1902*b*) that the arrangement of the sulci differs considerably from that of lemurs and apes, and still later (1908) that the pattern conforms to the Indrisine type. Reference to Fig. 6, however, shows how closely the brain of *Archaeolemur* approaches the simian type in its size, relative breadth, rich

fissuration, and the extent to which the cerebral hemispheres overlap the cerebellum. Although the sulci on the dorso-lateral aspect of the cerebrum can hardly be identified with any certainty, it is clear that, in general, they are disposed in a transverse rather than a longitudinal pattern. In this character they contrast sharply with the usual lemuroid arrangement and approximate to that of the Anthropoidea. Indeed, one particularly distinct sulcus (*C*) corresponds in its position and course to a fully developed sulcus centralis of simian type. On the other hand, the attenuated frontal lobes give the contour of the brain (as seen from above) a much more primitive appearance than that found in recent monkeys and recalls the general form of the cerebral hemispheres in *Tarsius*.

The fossil lemurs whose endocranial casts have been figured and briefly described in this note are all referable to the lemuriform division of the Lemuroidea, and there can be little doubt that *Adapis* represents a generalized form which bears an ancestral relationship to the Madagascan lemurs, fossil or recent. Thus it seems certain that the fissural pattern of the cerebral cortex in this group of Primates initially conformed to the generalized eutherian type, with a predominance of longitudinal folding. The same type of pattern was developed more elaborately in most of the extinct lemurs of Madagascar and is still found in most modern lemuroid genera. In the Pleistocene *Archaeolemur* and the modern *Indris*, however, the longitudinal has been replaced by a transverse pattern. This clearly has an important bearing on the validity of sulcal pattern as a criterion of morphological affinity, since it is apparent that within one subdivision of a suborder the pattern can undergo what appears at first sight to be rather a fundamental change. If the general disposition of sulci, however, is simply determined in ontogenesis by mechanical factors which influence the expansion of the cortex, and is not an expression of a morphogenetic tendency inherent in the cortex itself, such transformations may be expected to occur not infrequently in the course of evolution. The mechanical factors involved have yet to be analysed in detail, but there seem to be at least three which require consideration: the relative expansion of certain cortical areas, the relative size of the brain, and the shape of the skull. Of these, the first is perhaps the most important. Studies of the developing brain in the Moscow Brain Institute have recently shown that in man and monkeys the visual and frontal areas of the cortex undergo differentiation and expand earlier than they do in lower mammals (Sarkisov, 1944). It may be supposed that the precocious development of these areas sets up mechanical stresses in an anteroposterior direction which dominate the field of force within which the cortex undergoes its initial folding, leading to the production of the characteristic sulcal patterns. If a similar precocity is assumed to occur in *Archaeolemur* and *Indris*, it would explain the change-over in these lemuroids from the primitive longitudinal to a transverse arrangement of sulci, leading to a convolutional pattern which approaches that characteristic of the higher Primates.

SUMMARY

A study of endocranial casts of fossil lemuroids indicates that the convolutional pattern of the cerebral cortex conformed primitively to that of generalized eutherian mammals in the predominance of longitudinal sulci on the dorsolateral surface of the cerebral hemispheres. The development of transversely disposed sulci in certain genera is ascribed to the influence of mechanical factors during ontogenesis.

The author is indebted to Dr A. T. Hopwood for the endocranial cast of *Adapis parisiensis* and for providing facilities for the study of the casts of fossil lemurs of Madagascar; to the authorities of the British Museum for the loan of skulls of *Tupaia* and *Microcebus*; and to Prof. Cave for the loan of skulls of *Lemur*.

REFERENCES

Brodmann, K. (1908). *J. Psychol. Neurol., Lpz.*, **10**, 287.

Brodmann, K. (1909). *Lokalisationlehre der Grosshirnrinde.* Leipzig.

Burckhardt, R. (1901). *Anat. Ang.* **20**, 229.

Clark, W. E. Le Gros (1945). *Deformation Patterns in the Cerebral Cortex. Essays on Growth and Form.* Oxford Univ. Press.

Edinger, T. (1929). *Z. ges. Anat.* 1. *Z. Anat. EntwGesch.* **28**, 1.

Elliot Smith, G. (1902*a*). *Trans. Linn. Soc. Lond.* **8**, 319.

Elliot Smith, G. (1902*b*). In *Catalogue of Physiological Series of Comparative Anatomy.* Royal College of Surgeons Museum, **2**.

Elliot Smith, G. (1908). *Trans. Zool. Soc. Lond.* **18**, 163.

Forsyth Major, C. I. (1897). *Proc. Roy. Soc.* **62**, 46.

Grandidier, G. (1905). *Nouv. Arch. Mus. Hist. nat., Paris*, **7**, 1.

Neumayer, L. (1906). *N. Jb. Min. Geol. Palāont.* **2**, 100.

Sarkisov, S. (1944). Personal communication.

Vogt, C. & Vogt, O. (1907). *J. Psychol. Neurol., Lpz.*, 8. 277.

Zuckerman, S. & Fulton, J. (1941). *J. Anat., Lond.*, **75**, 447.

CLEAVAGE STAGES OF THE OVA OF THE HORSE, WITH NOTES ON OVULATION

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INTRODUCTION

There are few observations on the early development of the horse, and up to the present no account has been given of the early cleavage stages. Hausmann (1840) recovered ova from large ovarian follicles, but it was not until almost one hundred years later that Amoroso, Griffiths & Hamilton (1939) recovered an unsegmented living tubal ovum from the uterine tube. This ovum was photographed in the living state and then sectioned; it showed evidence of degeneration. Later in the same year, Day (1939) recovered an unsegmented egg.

FOLLICULAR GROWTH AND OVULATION

By rectal palpation of a mare's ovaries it is possible to follow follicular growth and ovulation during the oestrous cycle; by daily examinations an accurate estimate of the time of ovulation can be made (±6 hr.). The average length of oestrus is 6 days with great variations. As a rule one follicle gradually increases in size during oestrus and reaches an estimated diameter of 3·5–5 cm. just prior to ovulation. At first the follicle is quite tense, but within 12–24 hr. of ovulation becomes somewhat softened. At the time of ovulation the follicle bursts through the ovulation fossa and leaves a soft depression in the ovary. Within about 8 hr. the follicular cavity fills with blood clot, and for the next 10 hr. or so is soft and pliable to the touch until by 24–30 hr. after ovulation it is plum-like in consistency. It then becomes firmer and less conspicuous *per rectum* until by 4 or 5 days after ovulation it is no longer palpable, except that the ovary with the corpus luteum is normally about twice the size of the inactive ovary.

Insemination of mares with semen from a stallion of known good fertility gives equally good fertility results when insemination is carried out at any time from 0 to 72 hr. before ovulation.

The injection of pregnancy urine extract (B.D.H. 'Gonan') 500–1000 i.u. intravenously will cause ovulation (from the mare's ovary) within about 30 hr. providing there is a follicle of 3·0 cm. diameter in the ovary at the time of injection.

With a series of eight Welsh ponies it was decided by utilizing the facts mentioned above, to obtain tubal ova at different cleavage stages. Additional unsegmented eggs were recovered from a Shire and two thoroughbred mares (see Table 1).

METHOD

The mares were examined daily until a fairly large follicle was found to be present in one ovary. They were then inseminated with 10 c.c. of sperm from a Shetland pony stallion of known good fertility. One mare was allowed to ovulate naturally, but, to save repeated examinations, the other mares were injected intravenously with lutealizing hormone on the same day as insemination. Rectal examinations were then made as often as was necessary to estimate reasonably accurately the time of ovulation. The mares were killed at definite times after ovulation.

The eggs were obtained by flushing the uterine tubes with Locke's fluid into small watch-glasses. After being isolated they were transferred into several changes of Locke's fluid in order to separate them from small pieces of epithelial detritus. The eggs were photographed in the living state with a Vickers projection microscope at a magnification of 480. After photographing they were fixed in either Bouin's, Flemming's or Susa's fixatives, and then embedded by the agar technique as described by Samuel (1944) and sectioned at 7 μ.

UNSEGMENTED EGGS

There are six unsegmented eggs in our series, the measurements of which are given in Table 1. Three of the eggs were recovered from three ponies, the others from the Shire and two thoroughbred mares. From such a small series it is not possible to give a conclusive statement about differences in egg size in large and small breeds, but it may be noted that there is a striking similarity of size and so the results agree with what was found by Gregory (1930), who examined the living egg from three different genetic stocks of rabbit—giant strain, small Polish and mixed stock—and found that the eggs from all these rabbits were approximately of the same size and that no morphological differences could be detected.

In the living state the vitellus is composed of very many fatty globules which are so closely packed together that it appears opaque when examined with transmitted light and hence no nuclear detail is visible (Pl. 1, fig. 1). In this respect the horse egg resembles more closely that of the pig (Heuser & Streeter, 1929) than those of the other ungulates so far examined. It also shows a striking resemblance to the egg of the dog (van der Stricht, 1923), and to

that of the ferret (Hamilton, 1934). The vitellus in the normal egg, as is usual with tubal eggs, does not completely fill the zonal cavity. The perivitelline space is filled with finely granular material. In one egg fatty globules are being extruded into the enlarging perivitelline space (Pl. 1, fig. 4).

In the three degenerating eggs the cytoplasm shows clumping, and in the uterine egg the perivitelline space is obliterated. The zona pellucida is homogeneous and cumulus cells are absent. In the tubal eggs there is a thin coat of material resembling the albumen of the rabbit egg.

In the cleared agar whole mounts the cytoplasm has a granular appearance and, in normal eggs, the nucleus may be readily recognized (Pl. 1, fig. 2).

Table 1

	Stage of development	Vitellus: Measurements μ	Vitellus: Average μ	Zona measurements: Outside μ	Zona measurements: Average μ	Zona measurements: Inside μ	Zona measurements: Average μ	Volume of zonal cavity	Ovulation-killing interval in hr.	Dosage of Gonan in i.u.
Pony 1	Unsegmented	106×104	105	166×156	161	135×130	132·5	1,218,000	24–30	750
Pony 8	,,	104× 94	99	160×160	160	133×130	131·5	1,191,000	78–84	1000
Pony 3	In uterus	142×141	141	179×177	178	142×140	141	1,469,000	144–168	1500
Shire	,,	—	—	166×160	163	141×137	139	1,407,000	—	—
Thoroughbred A	Degenerating	90× 85	87·5	160×156	158	121×112	117	839,000	—	—
Thoroughbred B	,,	—	—	152×141	147	125×112	119	882,500	—	—
Pony 5	2-cell	—	—	156×141	149	133×119	126	1,047,000	24	Normal oestrus
Pony 2	3-cell	—	—	—	—	142×171	157	2,027,000	27–33	1000
Pony 7	4-cell	—	—	135×135	135	114×112	113	755,600	30–36	1000
Pony 4	5-cell	—	—	156×152	154	133×131	132	1,204,000	50–56	1000
Pony 6	Morula	—	—	179×154	167	148×127	138	1,376,000	98	1000

Range of diameter of vitellus 87·5μ (degenerating egg) to 141μ (egg recovered from uterus); in a normal egg shortly after ovulation 105μ.

Range of the outer diameter of zona pellucida is 135–178μ (average diameter 157·2μ); if the uterine egg is excluded the range is 135–167μ; average diameter 155μ.

Range of the inner diameter of zona pellucida (excluding the markedly oval egg pony no. 2) 113–141μ, average 131μ; if the uterine egg is again excluded the range is 113–138μ; average measurement for 9 eggs 128μ.

The zona pellucida has undergone a contraction. In the sectioned and stained material the cytoplasm is uniformly granular and shows no evidence of polarity. In each of the normal eggs there is a large vesicular nucleus lying at one side of the cytoplasm (Pl. 1, fig. 3). In none of the eggs were polar bodies found.

In all spontaneously ovulating mammals so far examined, with the exception of the dog, the formation and separation of the first polar body occurs when the egg is still in the ovary. The second polar spindle is then formed, but the separation of the second polar body is not effected unless fertilization supervenes. The ovum of the dog does not form the first polar body or even the chromosomes for the first maturation division until after it is shed (Evans & Cole, 1931). They state: 'It would appear that the polar body is not indeed formed for a day or two after ovulation.' They recovered eggs from the uterine tube, some with a vesicular nucleus and others with the first polar body and the second maturation spindle. The egg of the horse is also an exception to what has been found in most mammalian eggs. It could be argued that the first polar body had disintegrated and that the chromosomes had reconstituted themselves into a resting nucleus, but this is highly improbable. Another alternative might be that the administration of Gonan had prematurely caused ovulation. The observations of Hinsey & Markee (1933) indicate that the amount of pituitary secretions necessary to activate the egg is less than that required to produce ovulation. In their experiments ovarian follicles did not rupture in hypophysectomized rabbits as the result of the injection of Prolan, but polar body formation did occur. It seems probable that sufficient Gonan was present to cause polar body formation in the horse since it caused ovulation in all our mares on which it was used.

CLEAVAGE STAGES

Two-cell stage. This egg was ovulated spontaneously; on 4 August 1944 a follicle of 3·5 cm. was felt in the right ovary, and the mare was artificially inseminated. As the result of rectal examination on 8 August 1944 it was thought that ovulation had occurred 24 hr. previously, the mare was then killed.

The blastomeres in the living state do not fill the zonal cavity (Pl. 1, fig. 5). In the space unoccupied by the cells there is a considerable amount of granular material which had been eliminated from the egg as the result of deutoplasmolysis (see later). The cytoplasm of the blastomeres is similar to that of the unsegmented egg. There is a slight difference in the size of the cells but no difference in their texture. The sections show two blastomeres which are essentially similar in appearance (Pl. 2, figs. 6, 7).

Three-, four- and five-cell stages. A three-cell stage

was recovered at 27–33 hr. after ovulation, a four-cell stage at 30–36 hr., and a five-cell stage 50–56 hr. after ovulation. In all of these specimens, in the living state, there is an extensive perivitelline space filled with granular material. At the four-cell stage the cells are approximately the same size and are arranged at the apices of a tetrahedron (cross arrangement) as is typical for most eutherian eggs (Pl. 2, fig. 8). Sections of the four-cell stage are seen in Pl. 2, figs. 9 and 10. The arrangement of the cells at the five-cell stage is shown in Pl. 2, fig. 11. The examination of the sectioned material of the five-cell stage shows that the largest cell has a spindle of division (Pl. 3, fig. 12).

Fifteen-cell stage. This egg was recovered from the uterine tube 98 (± 6) hr. after ovulation. The cells which were closely packed together lay at one side of the zonal cavity. The remainder of the cavity is occupied by granular detritus which is even more extensive than at earlier stages (Pl. 3, fig. 13). When the egg was sectioned the cells were found to be similar in appearance except that one cell showed a spindle of division (Pl. 3, figs. 14, 15).

REMARKS ON CLEAVAGE

The examination of the few stages at our disposal shows that the cleavage of the egg of the horse is essentially similar to that of most mammals. For a eutherian egg there is, however, an extensive amount of deutoplasmolysis (or yolk elimination). This phenomenon was first described by O. van der Stricht (1909) in the egg of the bat (*Vesperugo noctula*), and since then has been described in other eggs: guinea-pig (Lams, 1913), dog (O. Van der Stricht, 1923), cat (O. Van der Stricht, 1923; Hill & Tribe, 1924), pig (Heuser & Streeter, 1929), and ferret (Hamilton, 1934). In the bat the process is found from the beginning of maturation, but becomes accentuated during fertilization and during the early cleavage stages. The yolk becomes detached mainly at the vegetative pole. In the egg of the other types described the process occurs after ovulation. We have no evidence of deutoplasmolysis of the horse egg until after ovulation, after which material is extruded in that part of the egg which is farthest from the nucleus. Even in the later stages the material is segregated more towards one side of the zonal cavity while the blastomeres lie more towards the other.

In *Dasyurus*, Hill (1910) found that the excess of yolk was eliminated at the upper pole prior to or simultaneously with the formation of the first cleavage furrow. In *Didelphys*, Hill (1918) found, owing to the absence of polar concentration of the yolk, that the surplus deutoplasm was eliminated from all the parts of the surface of the unsegmented egg and blastomeres.

The process of deutoplasmolysis appears to be related in some way to the amount of fat contained within the egg. In eggs which are particularly rich in fat, such as those of the horse, much material is eliminated during segmentation, in others, such as the mouse, where there is little fat, the process does not occur.

Van der Stricht (1923) states that though the ovum of the mammals is relatively poor in nutritive material it appears still to contain too much for the needs of the embryo, and so the excess is expelled into the perivitelline space.

SUMMARY

1. An account is given of living eggs of the pony and comparisons are made with eggs of other ungulates.
2. Measurements of the eggs are also given.
3. Cleavage stages (with 2, 3, 4, 5 and 15 blastomeres) are described and their approximate ovulation ages are recorded.
4. Deutoplasmolysis was found to be extensive.
5. The time of ovulation is discussed.

REFERENCES

Amoroso, E. C., Griffiths, W. B. & Hamilton, W. J. (1939). *Vet. Rec.* **51**, 168.
Day, F. T. (1939). *J. Agric. Sci.* **29**, 459.
Evans, H. M. & Cole, H. H. (1931). *Mem. Univ. Calif.* **9**, 65.
Gregory, P. W. (1930). *Contr. Embryol. Carneg. Inst.* **21**, 141.
Hamilton, W. J. (1934). *Trans. Roy. Soc. Edinb.* **58**, 251.
Hausmann, U. F. (1840). *Ueber die Zeugung und Entstehung des wahren weiblichen Eies bei der Säugetiere und Menschen.* Hannover.
Heuser, C. H. & Streeter, G. L. (1929). *Contr. Embryol. Carneg. Inst.* **20**, 1.
Hill, J. P. (1910). *Quart. J. Micr. Sci.* **56**, 1.
Hill, J. P. (1918). *Quart. J. Micr. Sci.* **63**, 91.
Hill, J. P. & Tribe, M. (1924). *Quart. J. Micr. Sci.* **68**, 513.
Hinsey, J. C. & Markee, J. E. (1933). *Amer. J. Physiol.* **106**, 48.
Lams, H. (1913). *Arch. Biol., Paris*, **28**, 229.
Samuel, D. M. (1944). *J. Anat., Lond.*, **78**, 173.
Van der Stricht, O. (1909). *Mem. Acad. R. Belg.*, 2nd series, **2**.
Van der Stricht, O. (1923). *Arch. Biol., Paris*, **33**, 229.

EXPLANATION OF PLATES

PLATE 1

Fig. 1. Photograph of a living unsegmented ovum of the pony (P 1) in Locke's fluid. Granular material is seen in the perivitelline space. ×480.

Fig. 2. Photograph of an unsegmented ovum of the pony (P 1) in agar. The nucleus is just visible. ×480.

Fig. 3. Section of an unsegmented ovum of the pony (P 1) with a large vesicular nucleus. ×520.

Fig. 4. Section of an unsegmented ovum of the pony (P 8) showing deutoplasmolysis. ×520.

Fig. 5. Photograph of a living two-cell stage ovum of the pony (P 5). Granular material is seen in the lower part of the perivitelline space. ×480.

PLATE 2

Figs. 6, 7. Two consecutive sections through the two-cell ovum shown in fig. 5. ×520.

Fig. 8. Photograph of a living four-cell stage ovum of the pony (P 7). ×480.

Figs. 9, 10. Two consecutive sections through the four-cell ovum shown in fig. 8. ×520.

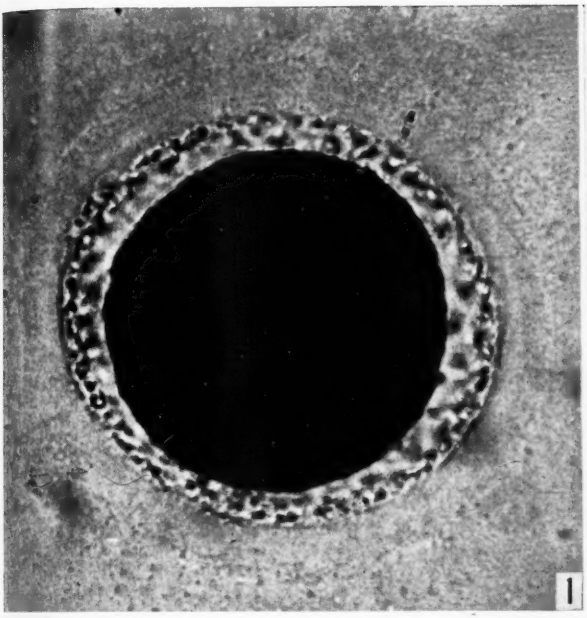
Fig. 11. Photograph of a five-cell stage ovum of the pony (P 4) in agar. ×480.

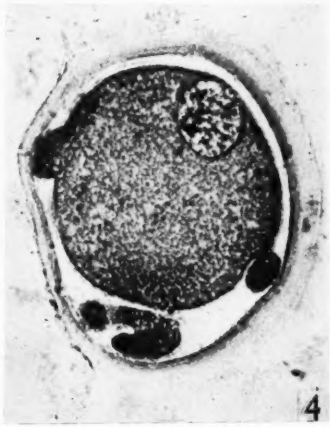
PLATE 3

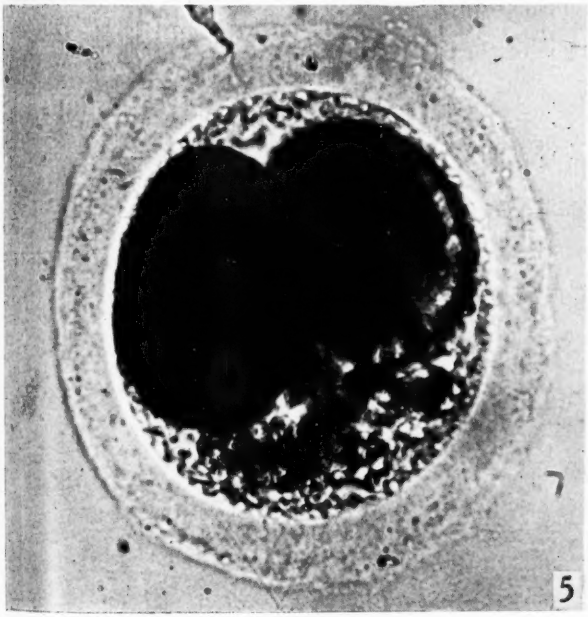
Fig. 12. Section through the five-cell ovum shown in fig. 11. ×520.

Fig. 13. Photograph of the living morula of the pony (P 6). It shows extensive deutoplasmolysis. ×480.

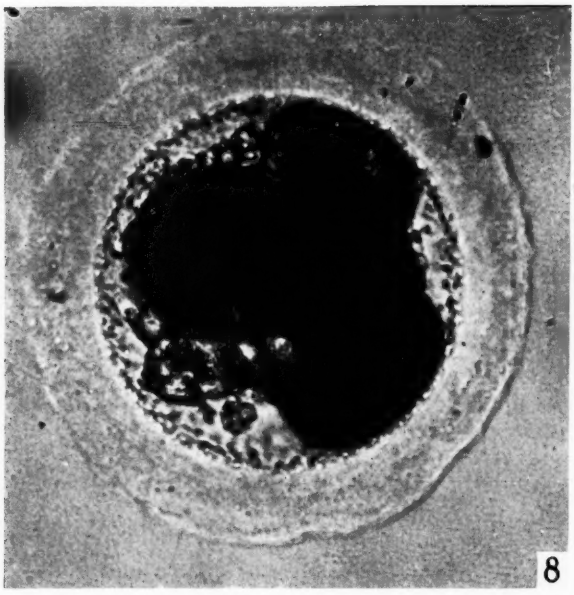
Figs. 14, 15. Two consecutive sections through the morula shown in fig. 13. ×520.

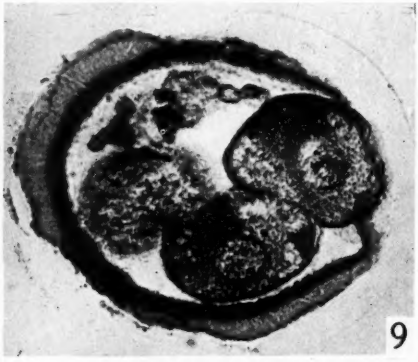


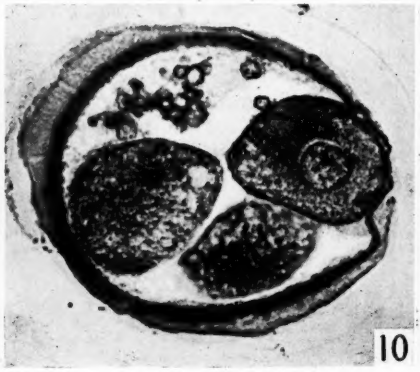




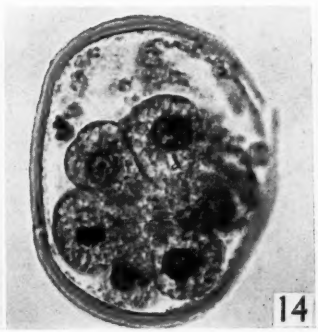
HAMILTON AND DAY—CLEAVAGE STAGES OF THE OVA OF THE HORSE, WITH NOTES ON OVULATION







HAMILTON AND DAY—CLEAVAGE STAGES OF THE OVA OF THE HORSE, WITH NOTES ON OVULATION



HAMILTON AND DAY—CLEAVAGE STAGES OF THE OVA OF THE HORSE, WITH NOTES ON OVULATION

UNIV. OF MICH.

THE TWO MAIN DIAMETERS AT THE BRIM OF THE FEMALE PELVIS

By C. NICHOLSON, *Moreton-in-Marsh District Hospital*

INTRODUCTION

The following is a quotation from a recent book (Smout, 1943) on the anatomy of the female pelvis: 'Internal Measurements...Diameters of the Brim ...Conjugate diameter, 11·25 cm....Transverse diameter, 13·1 cm.' This statement, which has been common to works on anatomy for more than 40 years, is faulty for three main reasons. (1) It gives no indication of the population to which it refers nor of the great variety to which these measurements are subject. (2) If, as we must presume, the statement applies to the Englishwoman the value for the conjugate diameter is probably much too low. (3) The length of the conjugate diameter is very considerably influenced by nutrition, and, in the absence of any large population which up to now can be considered as fully nourished in childhood, it is still quite impossible to determine the mean to which the measurement tends. These three statements are here examined in the light of a series of 640 measurements of the adult female pelvis made by radiology for obstetric purposes in Moreton-in-Marsh District Hospital.*

POPULATION AND METHOD OF MEASUREMENT

The population from which the measurements were taken consisted of all primigravidae presenting themselves for admission to the hospital for confinement. They constitute a fair sample through all strata of society from what is a predominantly rural population; this population has the great advantage that it is more homogeneous, both genetically and socially, than that derived from a hospital in a city or other large centre of population. The method of measurement, a stereometric one, has been published (Nicholson, 1943) in an endeavour to estimate the amount of the error of observation to which it is subject; the standard error of measurement for the conjugate and transverse diameters is there stated as less than 1 mm., and, judging from this statistical examination, there is no reason to suppose that the accuracy has been overestimated.

The conjugate diameter

The measurement dealt with in this series is not the true, but the obstetric diameter; the former is, of course, greater by some 5 mm. than the latter. If the 640 cases are separated into the years in which the measurements were made the following results (in mm.) are obtained for the means and standard deviations:

Year	1934	1935	1936	1937	1938
Mean	115·4	114·2	114·5	118·1	121·6
Standard deviation	11·2	10·1	9·8	9·8	10·1
Year	1939	1940	1941	1942	1943
Mean	121·2	121·0	119·3	120·9	118·2
Standard deviation	10·2	9·0	10·1	9·9	9·0

These values, especially the means for the first 3 years, are so irregular that it was thought worth while to analyse the variance for the whole series. The necessary figures for this are given in Table 1 in the Appendix. It is at once obvious that the variance 'between years', i.e. the variance of the means of the years, is so high as almost certainly to be significant. The probability of this variance is examined in Table 2, and it will be seen that it is only when we omit the first 3 years that this variance of the means ceases to be significant. We are therefore dealing with a population which is certainly not homogeneous with respect to the conjugate diameter at any rate. The test for homogeneity for the years 1937–43 in Table 2 is rather a negative test, and in Table 3 the probability of the distribution of the means and also the standard deviations for these 7 years is examined; the result is that we need not doubt that the population is really homogeneous with regard to the conjugate diameter for these years. At the same time the rather attractive theory that the length of the conjugate diameter rose from a low level in 1934–6 to a high level in 1938–40 and is once more falling is not disproved.

The transverse diameter

The measurements of this diameter may be treated in the same way as those of the conjugate; the figures by years are:

Year	1934	1935	1936	1937	1938
Mean	133·3	131·9	130·5	131·2	133·3
Standard deviation	8·0	7·5	6·7	8·4	7·1
Year	1939	1940	1941	1942	1943
Mean	132·1	131·3	130·2	130·8	129·9
Standard deviation	8·1	6·4	8·8	7·9	7·7

These figures are apparently much more regular than those for the conjugate; at any rate there is no such sudden change. The figures for the analysis of variance are given in Table 4 in the Appendix, and in Table 5 the probability of the variance of the means is seen not to be significant. The factor, then, which altered so markedly the length of the conju-

* Part of the cost of this inquiry has been met by a grant from the Medical Research Council.

gate for the earlier years is not operative in the case of the transverse diameter. As any estimate of the means of these diameters must be made from a homogeneous population the first 3 years must also be discarded here, and the probability that the variation in the mean and standard deviation are no greater than would occur by chance are tested in Table 6, and again we can be certain that we are dealing with a reasonably homogeneous population.

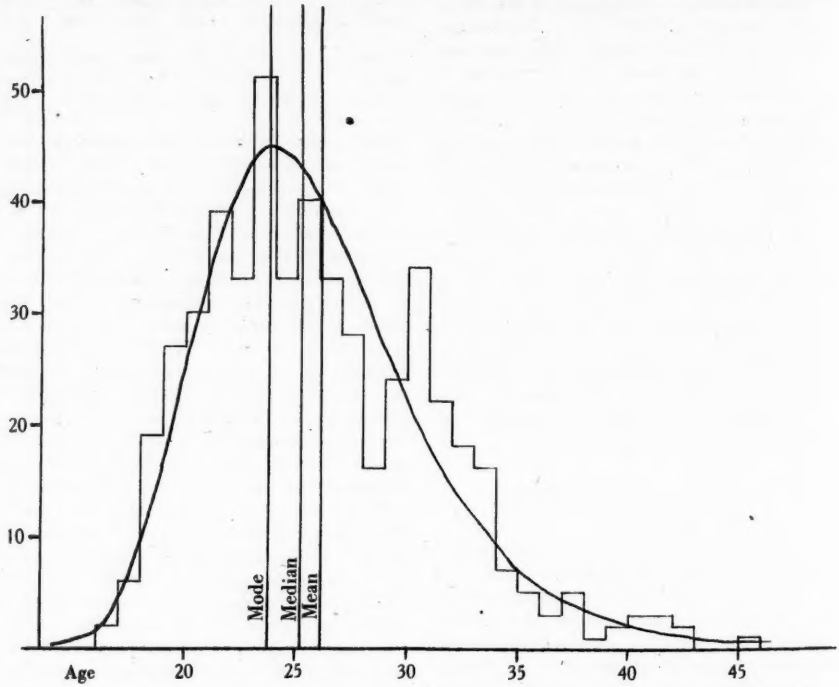


Fig. 1. Distribution by age of 503 primigravidae delivered at Moreton-in-Marsh District Hospital.

Correlation between conjugate and transverse diameters

The figures for the correlation coefficient are given in Table 7. For the 7 years the coefficient is 0·10, and this is just significant; that is, it would have occurred only once in twenty such trials if the diameters were independent. The probability that the figures for the different years accord with this slight positive correlation is tested and agreement is reasonable. The fact that the two diameters are virtually independent is of great importance in the classification of the pelvis by its shape; in the true rachitic pelvis there is undoubtedly a shortening of the conjugate diameter associated with a lengthening of the transverse, and it is a common fallacy that this strong negative correlation persists in the healthy pelvis; it is obvious that this false reasoning can lead to some absurd conclusions.

Variation in the conjugate diameter

It is impossible to leave the low level of the length of the conjugate diameter for the years 1934–6 without suggesting some theory which would account for the discrepancy. The obvious, and probably the correct, theory is that the period of malnutrition which occurred during the war of 1914–18 is wholly responsible. To assess the effect of this malnutrition information is necessary on two points: the age at which one would expect deformation of the pelvis to take place on account of subnutrition, and the age at which these women presented themselves as primigravidae. With regard to the first point there seems to be no definite pronouncement, but there is no doubt that frank rickets is a disease of the first 2 years of life, and it seems reasonable to suppose that deformation caused by malnutrition would take place in the early years of weight bearing; it is proposed to consider the age group 2–6 inclusive as liable to show this defect. With regard to the second point it is not now possible to trace the ages of all the women measured, but Fig. 1 shows the age

distribution of 503 primigravidae for a later period. It is now possible to state that of the primigravidae presenting themselves in 1934, 34% were in the sensitive age group in 1917 which was probably the year of the worst malnutrition; for 1937 this proportion had fallen to 15%, and for the following years it fell rapidly to zero. A similar fall in the percentage liable would be expected whatever figure is chosen for the liable age group.

A further argument for regarding the length of the conjugate as sensitive to malnutrition is that this figure is closely correlated with the general stature; a value for the correlation coefficient derived from 156 cases is as high as 0·5056, or, to put this correlation as a regression, if a woman has a conjugate diameter 1 cm. above average we should expect to find her taller than average by 7 cm. Of course some part of this increase in stature is due to the length of the conjugate itself, but that amount of increase would be not more than 0·5 cm. for an increase of 1 cm. in the length of the conjugate. It is generally accepted that most of the variation in stature that is not genetic in origin is in fact due to differences in nutrition, and it would not be beyond reason that the common factor shown by the correlation coefficient was indeed this factor of nutrition.

Functions derived from the two diameters

Taking the figures for 1937–43 for these two diameters, and making Sheppard's correction and a correction for the error of observation, we may now state that the following figures are correct for a rural population in England which escaped the effects of malnutrition due to the last war:

	Mean	Standard deviation	Expected in 100 cases Max.	Min.
Conjugate diameter	120·19	9·72	132	108
Transverse diameter	131·30	7·70	141	121

Obstetricians have of late devoted a great deal, probably too much, attention to the classification of the pelvis by its shape. Accepting the fact that the lengths of pelvic diameters, in common with other anatomical measurements, are normally distributed, we may from the given figures calculate the corresponding figures for the pelvic index which after all is the chief guide to the shape of the pelvis. They are as follows:

	Mean	Standard deviation	Expected in 100 cases Max.	Min.
Pelvic index	91·81	8·94	113	80

Of greater value to obstetricians is the area of the brim available for the passage of the foetal head; it has been shown (Nicholson, 1939) that a reasonable approximation for this is the area of the ellipse on the two diameters as principal axes. The figures for this function (in square centimetres) are as follows:

	Mean	Standard deviation	Expected in 100 cases Max.	Min.
Area at the brim	123·99	12·11	138	108

DISCUSSION

The female pelvis is, it must be remembered, a compromise; for the erect posture there can be no doubt that the male pelvis is architecturally sound; there cannot be two such different structures as the male and female pelvis both ideally built for weight bearing; the conclusion must be that the female pelvis has been compelled to sacrifice some of its architectural soundness because of its necessary use as a birth canal. It is, indeed, very likely that the form of the female pelvis is controlled by two separate gene complexes, one independent of sex and more or less identical with that in the male, and one sex-linked and peculiar to the female. It is easy to understand, then, that there must be a great deal of variety in the eventual form of the female pelvis; and further, that a pelvis not ideally designed for weight bearing should undergo deformation when it is also weakened by malnutrition.

Further evidence of the effect of differential nutrition, although the facts are not put in a mathematical form, may be gathered from a paper by Greulich & Thoms (1939) who contrast the pelvic form in a group of student nurses (who are drawn from a high social level in America) with that in the general hospital patient showing that the conjugate diameter tends to be longer in the former group. Another study of the female pelvis, this time from the London area, comes from Ince & Young (1940), whose figures accord well with mine; their figure for the mean of the obstetric conjugate is 118·3 mm.

If we add to the mean of the obstetric conjugate from this series 5 mm. for the difference between that and the true conjugate, it is startling to see that the mean for this diameter quoted in text-books of anatomy and obstetrics, and no doubt derived from measurements made on a series of cadavers of the lowest social level, is quite half an inch below that for a mixed rural population.

SUMMARY

Pelvimetry by radiology in 640 cases is analysed to show that the length of the conjugate diameter of the female pelvis is very sensitive to nutrition, and that the figure quoted in text-books of anatomy for this diameter is too low.

REFERENCES

GREULICH, W. W. & THOMS, H. (1939). *J. Amer. Med. Ass.* **112**, 485.
INCE, J. G. H. & YOUNG, M. (1940). *J. Obstet. Gynaec.* **47**, 130.
NICHOLSON, C. (1939). *J. Obstet. Gynaec.* **45**, 950.
NICHOLSON, C. (1943). *J. Obstet. Gynaec.* **50**, 37.
SMOUT, C. F. V. (1943). *The Anatomy of the Female Pelvis.* London.

APPENDIX

Table 1. *Conjugate diameter. Variance by years*

Year	Cases	$S(x)$	$S(x^2)$	Residual squares	Degrees of freedom	Mean square
1934	81	9,344	1,087,864	9958·6173	80	124·4827
1935	62	7,078	814,230	6196·3871	61	101·5801
1936	61	6,987	806,153	5855·1475	60	97·5858
1937	58	6,852	814,956	5474·8966	57	96·0508
1938	62	7,539	922,957	6238·9194	61	102·2744
1939	69	8,362	1,020,492	7114·5507	68	104·6258
1940	79	9,555	1,161,995	6323·7975	78	81·0743
1941	56	6,679	802,235	5644·9821	55	102·6360
1942	64	7,740	942,264	6207·7500	63	98·5357
1943	48	5,675	674,727	3776·4792	47	80·3506
			Between years	4913·1585	9	545·9065
Totals	640	75,811	9,047,873	67704·6859	639	105·9541

Table 2. *Conjugate diameter. Variance of the means of years*

Year group	Variance	Mean squares	n	z	P
1934–43	Between years	545·9065	9	0·8503	$<0·001$
	Within years	99·6691	630		
1935–43	Between years	528·1631	8	0·8522	$<0·001$
	Within years	96·0598	550		
1936–43	Between years	362·3714	7	0·6676	$<0·001$
	Within years	95·3713	489		
1937–43	Between years	124·8761	6	0·1364	$>0·20$
	Within years	95·0615	429		

Table 3. *Conjugate diameter. Probability of means and standard deviations*

Year	1937	1938	1939	1940	1941	1942	1943
Probability of mean	0·0854	0·2201	0·3541	0·4443	0·4506	0·5068	0·1404
Probability of standard deviation	0·9590	0·6749	0·4577	0·2649	0·6873	0·8537	0·3881

Total probability: Mean, 0·1835. Standard deviation, 0·9978.

Table 4. *Transverse diameter. Variance by years*

Year	Cases	$S(x)$	$S(x^2)$	Residual squares	Degrees of freedom	Mean squares
1934	81	10,793	1,443,221	5087·0617	80	63·5883
1935	62	8,176	1,081,552	3374·9677	61	55·3273
1936	61	7,958	1,040,926	2733·1475	60	45·5525
1937	58	7,608	1,002,005	4045·2759	57	70·9698
1938	62	8,267	1,105,355	3043·8871	61	49·8998
1939	69	9,118	1,209,394	4496·5507	68	66·1257
1940	79	10,375	1,365,761	3221·4430	78	41·3006
1941	56	7,292	953,790	4267·4286	55	77·5896
1942	64	8,370	1,098,526	3886·9375	63	61·6974
1943	48	6,234	812,450	2809·2500	47	59·7713
			Between years	819·5487	9	91·0610
Totals	640	84,191	11,112,980	37785·4984	639	59·1322

Table 5. ***Transverse diameter. Variance of the means of years***

Year group	Variance	Mean squares	n	z	P
1934–43	Between years	91·0610	9	0·2198	Between 0·05 and 0·20
	Within years	58·6761	630		

Table 6. ***Transverse diameter. Probability of means and standard deviations***

Year	1937	1938	1939	1940	1941	1942	1943
Probability of mean	0·8606	0·0280	0·3481	0·9896	0·2455	0·5341	0·1658
Probability of standard deviation	0·3544	0·2859	0·5605	0·0111	0·1493	0·9012	0·9681

Total probability: Mean, 0·2434. Standard deviation, 0·1880.

Table 7. ***Correlation between conjugate and transverse diameters***

Year	Cases	$S(x-\bar{x})(y-\bar{y})$	r	z	P
1937	58	−966·3793	−0·2054	0·2072	0·0226
1938	62	1113·4656	0·2555	0·2613	0·2162
1939	69	1145·1159	0·2025	0·2053	0·3937
1940	79	855·3165	0·1895	0·1918	0·4251
1941	56	1087·7857	0·2216	0·2254	0·3625
1942	64	−755·8750	−0·1539	0·1551	0·0461
1943	48	706·3750	0·2168	0·2203	0·4606
Totals	436	3185·8041	0·0965		

Total probability, 0·0475.

Notes on the tables

Tables 1 and 4 merely give the observed figures from which the other tables are calculated.

Tables 2 and 5 are a comparison between two variances which is calculated as a z, and the probability is taken from the tables.

For Tables 3 and 6 the total residual squares are partitioned into three parts for each year in turn:

(*a*) The part due to the year in question.
(*b*) The part due to the remaining years.
(*c*) This leaves a part with only 1 degree of freedom due to the difference between means.

For the probability of the mean, then, $\sqrt{[c/(a+b)]}$ is a t, but as the numbers involved are sufficiently large the probability is calculated as though it was a normal deviate. For the probability of the standard deviation a z is calculated from the ratio of a to b, and this is again treated as a normal deviate with the appropriate standard deviation. For the total probability, twice the natural logarithm of each separate probability with changed sign is a χ^2 for 2 degrees of freedom; the sum of these for the 7 years is then a χ^2 for 14 degrees of freedom and the total probability is taken from the tables.

In Table 7 the probability for each year is calculated by dividing the difference of the z for each year and the z for a coefficient of 0·10 by its appropriate standard deviation and treating the result as a normal deviate; the total probability is calculated as before.

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